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Contents

1

Serological Correspondence Among Horseshoe "Crabs" (Limulidae)[1]

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(Plate I: Text-figures 1 & 2)

INTRODUCTION

THE FEW RESEARCHERS, Graham-Smith (1904), Boyd (1937), Wilhelmi (1942, 1944) and Leone & Webb (1952), that have reported on systematic aspects of the blood serum of horseshoe "crabs," have all compared *Limulus* serum with that of animals outside of the family. Since the present report is the first on the comparative serology of the Limulidae, it constitutes an introduction to the serological relationships among horseshoe "crabs." Three of the four extant species, representing the two subfamilies, were serologically compared: the North American species *Limulus polyphemus* (Linnaeus) Müller, Limulinae, and two Indo-Pacific species, *Carcinoscorpius rotundicauda* (Latreille) Pocock, and *Tachypleus gigas* (Müller) Leach, Tachypleinae. The fourth, the remaining Asiatic species, *Tachypleus tridentatus* Leach, was not studied.

The data, obtained by turbidimetric measurements and agar-diffusion records of the precipitin reaction between antigens and antibodies, were limited by the available supply of serum from the Indo-Pacific species.

Our serological findings provide a basis for a more comprehensive study on the systematics of the Limulidae. There is questionable support for the taxonomy proposed by Pocock (1902), who divided into three genera the four extant species previously confounded under *Limulus*.

MATERIALS AND METHODS

Hemolymph samples were collected from adult limuli in eleven populations of *Limulus*, from Florida to Maine, during the summer of 1953. Sera for this study were selected from animals in four widely separated populations: Pleasant Bay, Massachusetts; Providence River, Rhode Island; Miles River, Maryland; and Sarasota Bay, Florida. Sera from two of the three Indo-Pacific species, *C. rotundicauda* (samples from eleven specimens) and *T. gigas* (one sample), were obtained by Dr. D. S. Johnson and his associates in the Department of Zoology, University of Malaya. Without this generous assist from Dr. Johnson the present study would not have been possible; the author owes him a personal note of gratitude. Similar contacts with other researchers, to obtain *T. tridentatus* serum, proved nonproductive.

The hemolymph was preserved for study in the following manner (see Boyden, 1953, for general procedure). (1) A horseshoe "crab" was held in ventriflexion over a large glass beaker, or a funnel, and the arthrodial (dorsimesal) membrane in the hinge region cut deeply to puncture the underlying heart. Hemolymph usually flowed rapidly, directly from the heart; the flow could be increased by slowly moving the opisthosoma up and down like a bellows. (2) The hemolymph was stored overnight in an ice chest or a refrigerator to allow the amoebocytes to coagulate and form a "clot." (3) Then, after the clot formed, the serum was decanted into a graduate. (4) A stock solution of merthiolate (1 gram merthiolate powder in 100 milliliters of distilled water) was then added, 1 milliliter of the stock solution to each 49 milliliters of serum and the solution shaken well. (5) The merthio-

lated serum was bottled and stored in a cold room until used (temperature regulated at 1°C.).

Antisera to the serum of female *Limulus* from six different populations and the Tachypleinae sera were produced, using rabbits as producers. A reciprocal testing program was followed, limited only by the small amount of Tachypleinae serum available. Full reaction curves for each of the antigens were run on the Libby photronreflectometer (photron'er). In graphing the results, galvanometer readings on the photron'er were expressed as turbidity units along the ordinate, antigen concentration as antigen dilution along the abscissa. Each successive cell of antigen dilution, 1 through 15, contained one-half as much antigen as the preceding cell. The first cell, 1, was assumed to contain 5% antigen, or a titer of 1/20. Thus, cell 15 has an assumed antigen titer of 1/327,680. The exact protein concentration is not critical when whole titration curves are available for comparison. Total turbidity values for each curve were obtained by adding all the individual turbidities of each antigen dilution tube in the test. A value of 100 percent. was assigned to the area under the homologous curves and the heterologous values then expressed as percentages of the homologous total.

These serological tests were conducted at The Serological Museum, Bureau of Biological Research, Rutgers—The State University of New Jersey, under the direction of Drs. Ralph J. DeFalco and Douglas G. Gemeroy in 1954 and 1955. The techniques and procedures elaborated by Dr Alan A. Boyden, director of The Serological Museum, and co-workers (Boyden & DeFalco, 1943; Bolton, Leone & Boyden, 1948; and Leone, 1949, 1950) were used. The author is grateful to Dr. Boyden for reviewing the manuscript of this report.

Another measure of the precipitin reactions among Limulidae sera and antisera were obtained from a series of tests using the double-diffusion, Jennings-modified (Jennings & Malone, 1954; Jennings, 1954), three-depot method of Ouchterlony (1949). The desired test combinations of sera and antisera, each reactant placed separately in the corner reservoirs of a triangular plastic plate, separately diffuse through the agar. The diffusing reactants immediately combine in the region of equivalent concentrations (Munoz, 1954). At first invisible, this combination appears in time as a band or zone of precipitin which can be photographed. Dr. Sheldon A. London conducted these tests at the University of Delaware in 1957, in conjunction with a problem on micro-

bial serological correspondence. The author is indebted to Dr. London for the photographs and the data he obtained.

RESULTS

Reciprocal precipitin reactions between the sera and antisera of three species of Limulidae, *L. polyphemus, T. gigas* and *C. rotundicauda,* are summarized in Tables 1 and 2, and are shown on graphs (Text-fig. 1), a diagram (Text-fig. 2) and photographs (Plate I).

The curves (Text-fig. 1) obtained from the precipitin tests are typical unimodal curves which show no departure in spatial arrangement from a typical reaction curve (see for example: Leone, 1949; Boyden & DeFalco, 1956). The relative positions of the peaks of the curves are also typical, with the peaks of the heterologous curves usually to the right of and exceeded by the peak of the homologous reaction.

Turbidimetric results are summarized by a diagram (Text-fig. 2) indicating the serological distance between the species using a modification of Boyden's (1932) method. When the reaction values between two species are averaged and subtracted from 100, a serological "yardstick" is obtained which indicates the relative distances between the species. Thus the triangle in Text-figure 2B gives the relative distance between the three species according to a turbidimetric measurement of the precipitin reaction of their serum proteins in the reciprocal tests.

Reactions among sera and antisera for three *Limulus* from widely separated populations produce the typical homologous pattern of coalesced zones and form four precipitin bands in the agar plates (Plate I, Figures A, B). The crossed zones produced by tests between the three species show the unrelated character of at least two major components of the reactants (Plate I, Figures C, D) or one component (Plate I, Figures E, F). The *Tachypleus-Carcinoscorpius* reactants appear to produce the coalesced zones typical of strong serological correspondence (Plate I, Figures G, H). The asymmetry of the zones is ascribed to unequal concentrations of the reactants, with zone displacement toward the reservoir containing the reactant of lesser concentration.

DISCUSSION

An examination of the turbidimetric data (Table 1 and Text-fig. 1) reveals the marked difference in the magnitude of the reaction of each of the antigens to the antisera and the shift to the right of the heterologous reaction curves in the region of antigen excess.
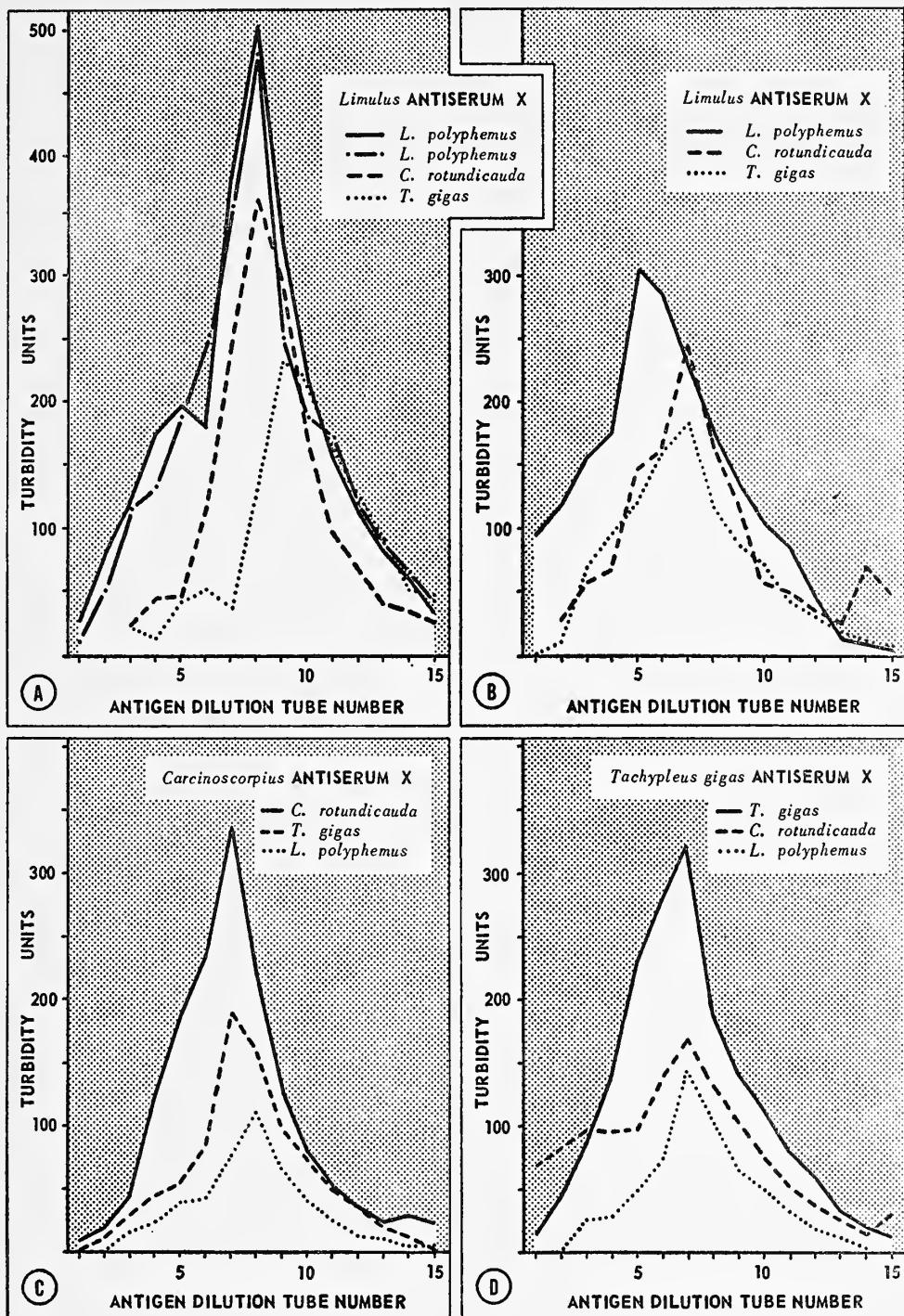
TEXT-FIG. 1. Precipitin titration curves showing the order of serological relationships among three species of horseshoe "crabs": *Limulus polyphemus, Carcinoscorpius rotundicauda* and *Tachypleus gigas*. The antisera and test sera (antigens) are given in the legend for each series of curves. The area under the homologous reaction curve is highlighted by the shaded background.

TABLE 1. RELATIVE AMOUNTS OF PRECIPITIN REACTION, RECORDED AS TURBIDITY
IN PHOTRONREFLECTOMETER TESTS

These four sets of data (A-D) are represented graphically in Text-fig. 1.

Antiserum	Antigen	Peak Tube Number	Turbidity Units		
			Peak	Total	Percent. of Homologous Reactions
A. *L. polyphemus*	*L. polyphemus**	(8)	501	2641	100
	*L. polyphemus**	(8)	481	2502	95
	C. rotundicauda	(8)	361	1556	59
	T. gigas	(9)	230	1212	46
B. *L. polyphemus*	*L. polyphemus*	(5)	305	1924	100
	C. rotundicauda	(7)	247	1284	67
	T. gigas	(7)	183	1025	53
C. *C. rotundicauda*	*C. rotundicauda*	(7)	336	1549	100
	T. gigas	(7)	189	871	56
	L. polyphemus	(8)	112	477	31
D. *T. gigas*	*T. gigas*	(7)	320	1769	100
	C. rotundicauda	(7)	171	1208	68
	L. polyphemus	(7)	143	616	35

* Serum from specimens in two geographically different populations.

A comparison of all the reaction curves suggests that the several different rabbits employed in the production of the antisera reacted to the sera and produced comparable specificities of antibodies. The shift to the right of the heterologous curves, with respect to the homologous reaction, generally denotes a lesser amount of serological reaction between the heterologous sera and the test antisera. We are concerned here, however, with the relative placement of the species, from the homologous to the lesser reaction of the heterologous antigens, in each of the apparently linear serological series. These series are the basis for the two-dimensional diagram (Text-fig. 2) of the relationships among the three species. For a general discussion of the principles of systematic serology and the im-

plications of the results of precipitin testing see Boyden (1942).

The serological placement of *L. polyphemus* slightly closer to *C. rotundicauda* than to *T. gigas* (Table 2 and Text-fig. 2B) requires further testing. Evidence (Shuster, 1958) indicates that *L. polyphemus* has a greater correspondence in morphometric and morphological characters with the genus *Tachypleus* than with *Carcinoscorpius*. Data for a definitive systematic evaluation, however, are not available. For instance, it is possible that *T. tridentatus,* which was not tested, is closer serologically to *Limulus* than *T. gigas* is. Further, since the Indo-Pacific serum supply was limited and only two rabbits were employed, one each, for the production of the antiserum to *T. gigas* and *C. rotundicauda,* a sharply defined serological relationship is impossible at this time.

The turbidimetric data are consistent, as the reciprocal tests show (Table 2). The greater reaction between *Limulus* serum and the antiserum of the two other species (46 and 59% or 53 and 67%), than that from the reciprocal reactions (35 and 31%), may indicate that the *Limulus* serum has one or more additional chemical components. The number of these components is suggested by several kinds of studies.

According to Allison & Cole (1940), hemocyanin is the only protein present in the serum of *Limulus polyphemus* after complete removal of the clot. They also noted that the clotting process, which involves the amoebocytes, does not

TABLE 2. SUMMARY OF THE TURBIDIMETRIC DATA ON THE RECIPROCAL PRECIPITIN REACTIONS, RECORDED AS PERCENT. OF THE HOMOLOGOUS REACTION. These data are graphically portrayed in Text-fig. 2.

Antiserum	Antigen		
	Limulus	*Carcinoscorpius*	*Tachypleus*
L. polyphemus	100	59	46
	100	67	53
C. rotundicauda	31	100	56
T. gigas	35	68	100
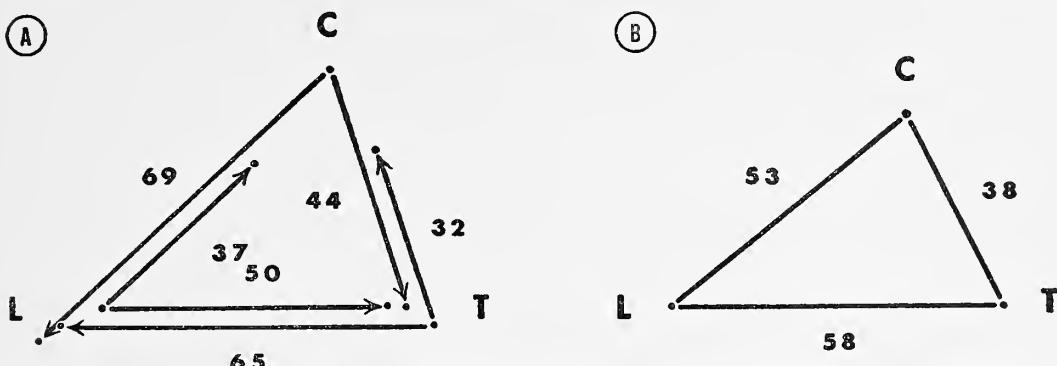
TEXT-FIG. 2. Two stages in the construction of a "serological yardstick" diagram show the relative distances between the three species: *Limulus polyphemus, Carcinoscorpius rotundicauda* and *Tachypleus gigas.*

remove any appreciable amount of hemocyanin from the serum. *Limulus* hemocyanin exists, within the pH range of 5.2-10.5, in four different and stable molecular species, but dissociation and a fifth component appear when the pH is less than 5.2 (Eriksson-Quensel & Svedberg, 1936). The electrophoretic pattern of *Limulus* hemocyanin reveals at least five components (Deutsch & McShan, 1949) and at least four prominent entire bands are revealed by the homologous test for *Limulus* in the agar-diffusion precipitin technique. The later technique reveals one and perhaps two major reaction bands that do not coalesce in any of the reciprocal reactions between *Limulus* and the two Indo-Pacific species. Reactions between only *Tachypleus* and *Carcinoscorpius* give entire but fewer bands.

Boyden (1943) found that the serological correspondence among marine crustaceans of the same genus averaged 46%. Later, in similar studies, Leone (1949, 1950) distinguished between species of the same genus within certain families of Crustacea. In his studies the magnitude of serological correspondence between crustaceans of the same genus was as low as 31%, but most values were above 70%, with some as high as 89% for closely related species. In our Limulidae study the heterologous reactions ranged from 30 to 67%. Although not directly comparable, the serological distance between species of the same genus of marine crustacea, when used as a "ruler" for comparison with the values among the Limulidae, suggests that the three species studied are congeneric.

Interpretation of the "distances" provided by the "serological ruler" is arbitrary, since "distance" depends upon a sliding scale which in turn is an expression of the specificity, *i.e.,* the discriminating capacity, of the antiserum which varies from antiserum to antiserum. Also, there are too few species and the present data are too scanty to establish more definite serological measurements of either species or genera within the Limulidae. Further, the best available reference for comparison is a distant taxonomic group comprised of many families, the Crustacea. The Limulidae is a very small taxon by comparison, but it is one that has roots in an old history, as measured by the geologic age of the Xiphosura, and one that reflects a conservative evolution.

If we consider that the present serological findings coincide with the current sub-Limulidae taxonomic categories given in the beginning of this report, then the serological distance between species, genera and families is indeed narrow.

SUMMARY

From the turbidimetric measurements of precipitin reactions among the Limulidae sera and the rabbit-produced antisera it can be concluded that:

1. The precipitin reactions produced typical titration curves.

2. No demonstrable differences were found in the homologous reactions based on *Limulus* sera from different populations.

3. The sera of the two Indo-Pacific Limulidae tested, *Carcinoscorpius rotundicauda* and *Tachypleus gigas*, are readily distinguished from the sera obtained from different populations of *Limulus polyphemus*.

4. Serological correspondence is greatest between the two species of Tachypleinae, but *C. rotundicauda* may be serologically closer than *T. gigas* to *L. polyphemus*.

5. The three species of Limulidae are congeneric when compared to the same magnitude of serological correspondence among marine Crustacea.

6. The taxon including the Limulidae is limited in number of species, yet it exhibits a long geologic history and a conservative evolution. If the current classification is correct, wherein three of the four species are not congeneric, then the taxonomic categories of the extant species, genera and families are indeed narrow.

7. The results and other information reviewed in the discussion suggests that *Limulus* serum may have one or more components not present in the sera of the two Indo-Pacific species.

Data from agar-diffusion records of the precipitin reaction revealed:

1. Four major bands of reaction or components in *Limulus* homologous reactions.

2. A lack of correspondence for one and perhaps two major components between the Indo-Pacific species and *Limulus*.

3. An apparent complete correspondence between the two species of Tachypleinae.

The present study was limited by the lack of an adequate supply of sera from the Indo-Pacific species. More extensive serological studies would be of great value in interpreting the systematics and evolution of the Limulidae. These studies should include serum of the species *Tachypleus tridentatus* and employ, for example, the immunoelectrophoretic method (first used by Grabar & Williams, 1953, and emphasized as a requirement in systematic serology by Williams, 1956), among other techniques.

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EXPLANATION OF THE PLATE

PLATE I

These retouched photographs of triangular serum-agar plates show the visible bands of precipitin reaction among the three species: *Limulus polyphemus, Carcinoscorpius rotundicauda* and *Tachypleus gigas*. The set of three letters around each triangle indicate the side from which the serum of each species (designated by CAPITAL LETTERS: L, C, and T) or antiserum to each species (lower case letters: l, c, and t) diffused. The eight sets of reactions, designated by the letters A through H, are described in the text.

SEROLOGICAL CORRESPONDENCE AMONG HORSESHOE "CRABS" (LIMULIDAE)
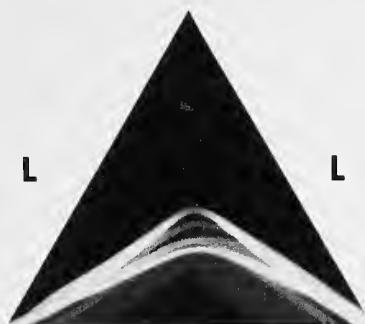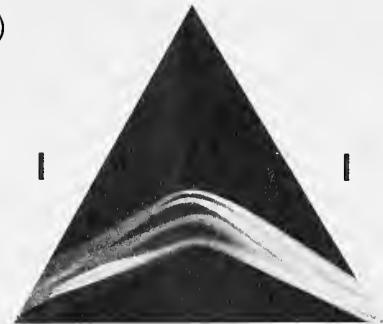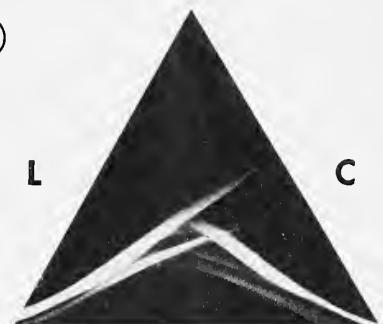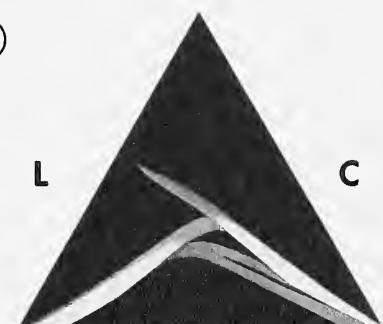
2

Relative Abundance, Microhabitat and Behavior of Some Southern Appalachian Salamanders[1]

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(Text-figure 1)

INTRODUCTION

SOME 44 years have elapsed since Emmett Reid Dunn described *Plethodon yonahlossee* and discussed the relative abundance and behavior of the salamanders associated with it in the Linville, Avery Co., North Carolina, area (Dunn, 1917). Many of Dunn's observations concerning the plethodontid salamanders were supplemented in a later publication (Dunn, 1920) and by other workers (Breder & Breder, 1923; Bailey, 1937; Gray, 1939; Wood, 1947; Hairston, 1949; and Pope, 1950).

The type locality of *Plethodon yonahlossee* is given as "near the Yonahlossee Road about 1½ mile from Linville, North Carolina" (Dunn, 1917). The general area in which Dunn worked "most of the time in sight of the road" embraces a hill which "rises to about 4,400 feet," with the road having an average altitude of 4,100 feet. In August, 1960, the authors made observations and collections along the Yonahlossee Road (frequently referred to as "Old Yonahlossee Road") in the vicinity of View Rock, a vantage point overlooking N. C. Hwy. 220. The collection was prompted by a need for an ontogenetic series for investigations of osteology and myology (DBW), comparative physiology (JAM) and behavior and periodicity (REG).

This paper presents (1) a report of the collection, (2) a comparative description of the type

locality after 44 years, and (3) a discussion of the habitat, relative abundance and behavior of collected salamanders.

DESCRIPTION OF THE COLLECTING STATIONS

Dunn (1917) gives no detailed description of the flora of the type locality for *Plethodon yonahlossee* nor of the surrounding area, but we infer from his remarks (see p. 595) that the mixed mesophytic forest typical of the undisturbed southern Appalachian Mountains prevailed.

Our collections were made at two stations. The first was a gentle slope 0.5 miles below View Rock (toward Linville); the second was 0.6 miles above View Rock and approximately 1.5 miles from the Linville entrance to the Yonahlossee Road. In our judgment, the second station embraces the type locality as designated by Dunn. The area has been subjected to at least one lumbering since Dunn's visit, as indicated by the presence of well-decayed stumps up to four feet in diameter and numerous fallen logs.

The flora of both stations consists of a second growth mixed mesophytic forest, aptly described as a "rich woods." At the first locality the collecting was concentrated along and on the downhill side of the Yonahlossee Road. We estimate the area covered as one acre. No detailed notes of the flora were made, but the area had less understory, fewer stumps and logs than the second locality.

Distinctive landmarks encountered during the collecting permitted us to measure the total area covered at the second locality. We collected an

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area on the southeast slope (15% gradient) 100 × 200 yards above the road, and 100 × 100 yards below the road. The elevation of the present road is 4,300 ft. at this point. The area was bounded on the east by a fast-flowing stream and on the west by a dense understory of nettle which prohibited effective collecting. The present road bed was laid down to the north, or uphill, from that travelled by Dunn, and remnants of the old roadbed formed a distinctive landmark below the present road, a distance of 100 yards. The total area in which we collected is approximately 2.1 acres.

The flora of the second station was examined both at the time of our collection and on a subsequent trip over the surrounding area. The canopy is dominated by a mixture of red and white oaks, maples, buckeyes, ironwood, gum and tulip trees. A few hemlocks are scattered through the area. The understory is sparse although seedlings of the above, plus chinquapin, catbriar and an occasional rhododendron thicket are present. The most prevalent plants composing the herbal layer are jewelweed, nettle, shield fern, pipsissewa, goldenrod, twayblade, bell flower and clumps of pinesap.

The sandy surface is covered by a 3- to 4-inch loam on top of which leaf litter, minimally 3 inches in depth, occurs. Stumps and logs in various stages of decay are numerous and seem to constitute important physical features of the habitat of *Plethodon yonahlossee*. Occasional outcrops of the underlying granite occur. The leaf litter, logs, stumps, rock outcrops and bases of plants conceal the openings to the refugia of the salamanders.

METHODS

Daytime collecting was restricted to the hours of 4:00 to 6:15 P.M. Both stations were examined. Six man-hours were spent hand-collecting salamanders exposed by log rolling and rock turning.

Night collecting with light from two headlamps and a Coleman gas lantern was carried out between 8:30–12:00 P.M. The salamanders were collected by hand, but few objects were turned. The entire night sample was taken from the station 0.5 miles above the View Rock. In all, 10.5 man-hours were spent in collecting at night.

The two samples were maintained separately, so as to permit a comparison between day and night sampling.

THE SAMPLE

The total number of salamanders taken, in 16.5 man-hours of collecting at the two stations,

was 661. The sample includes the following forms: *Diemictylus v. viridescens, Desmognathus ochrophaeus carolinensis, D. m. monticola; Plethodon c. cinereus, P. g. glutinosus, P. yonahlossee, P. jordani metcalfi,* and *Eurycea bislineata wilderae.*

A difference between day and night collecting was first noted by Bailey (1937), who obtained much better results for *P. yonahlossee* at night. Nocturnal collecting is effective for almost all species of salamanders; however, no quantitative reports of collecting results have been made. Diurnal collecting yielded 28.3 salamanders per man-hour, whereas nocturnal collecting produced 46.8 per man-hour. In addition, habitat disturbance is minimal during night collecting. The destruction of habitat during diurnal collecting activities has led to reduction of population size (as measured by availability) in some areas that have been visited from time to time by one of us; other areas that have been collected with the same intensity at night with little or no habitat destruction continue to produce large samples of animals.

Another important point not mentioned by previous workers is the composition of a sample as affected by difference in time of collecting (Table 1). While it can be argued that animals taken during the day are not available for sampling at night, only a part of the daytime sample (in our best judgment, 20 per cent.) was taken from the same locality as was sampled at night. The difference in sample composition is striking. If the species were ranked from most abundant to least abundant, not one of the six most abundant taken in the daytime would retain its position when based on nocturnal abundance. This difference is a result of the behavior and consequent availability of the species encountered. *Desmognathus* seemed to occupy the most superficial cover of all species and consequently was more available in the daytime than when it was active at night. *Plethodon yonahlossee* and *P. jordani* retreat into deep burrows and hence are not discovered by rock rolling, log turning, etc., as is *P. glutinosus,* which occupies a more superficial diurnal refuge. Note that the three most abundant plethodons represent only 36 per cent. of the diurnal sample, but 72 per cent. of the nocturnal sample.

RELATIVE ABUNDANCE

Although Dunn collected for three days and we for only one, we believe that the results are comparable because the mean number of individuals for one of Dunn's days is equivalent to our single day. Dunn's sample of August, 1916,

TABLE 1. PERCENTAGE COMPOSITION OF SAMPLE BY DAY, BY NIGHT,
AND TOTAL COMPARED WITH THAT OF DUNN (1917)

Species	Percent of Total		D + N*	Dunn, 1917
	Day	Night		
Diemictylus viridescens (eft)	1.8	0.0	0.5	9.5
Desmognathus ochrophaeus	57.6	24.2	32.8	29.3
Desmognathus monticola	2.9	1.0	1.5	0.0
Plethodon cinereus	1.2	2.3	2.0	10.4
Plethodon glutinosus	10.6	6.7	7.7	10.2
Plethodon yonahlossee	6.5	16.7	14.1	5.0
Plethodon jordani	18.8	48.7	40.9	32.6
Pseudotriton ruber	0.0	0.0	0.0	0.2
Eurycea bislineata	0.6	0.4	0.5	2.8
Total number individuals	170	491	661	462

*Day and night combined.

probably was made during diurnal forays. There is no indication of time of collecting in either his 1917 or 1920 paper, and night collecting for reptiles and amphibians has been prevalent only in the last twenty years. In view of these points, we believe that the only valid comparison that may be drawn is between our daytime data and those of Dunn. Several differences between the two sets of data (Table 1) may be noted, including (1) an increase in the percentage of *Desmognathus ochrophaeus* in the sample (29.3 to 57.6%); (2) a decrease in the percentages of *Plethodon cinereus* (10.4 to 1.2%) and *P. jordani* (32.6 to 18.8%); and (3) the relative constancy of *P. yonahlossee* and *P. glutinosus*. *Eurycea* was noticeably rare, but this form is lacking in samples from other areas of the southern Appalachians which in recent years had been very productive.

The data may indicate either a gradual shift in the composition of the population, or a short term fluctuation that may be cyclic. The latter, in view of previous collecting (1948-50, by REG), seems to be the case for *Eurycea*.

Whatever drastic effect lumbering might have had upon the area has been negated by subsequent succession, although one is tempted to suggest that the 20 per cent. decrease in the combined plethodon group (primarily *P. cinereus* and *P. jordani*) from that of 44 years ago may be attributed to lumbering. At the same time, the addition of stumps and logs in various stages of decay would seem to enhance the position of *P. yonahlossee*, since these appear to represent conspicuous elements in its habitat (Pope, 1950).

Pope (1950) discusses the relative abundance of *Plethodon yonahlossee*, *P. glutinosus* and *P. j. metcalfi*. His daytime data (obtained in July

and August, 1949) for *P. yonahlossee* and *P. glutinosus* are converted to percentages and compared to that of Dunn (1917 and 1920, combined) and our data for 1960 (Text-fig. 1). The percentage distribution for all daytime samples (except that of Pope from Comers Rock) falls into the same general pattern. However, we believe that the best measure of relative abundance lies in a combined collecting, one which samples the individuals not only in their refugia, but also as they are active on the surface. A reversal of the pattern occurs when our data are pooled to illustrate this point. The reversal would be even greater if the individuals taken at night were considered separately. The latter procedure would be misleading, but perhaps not as much as consideration of a daytime sample alone.

MINIMAL AVAILABLE DENSITY

Because of the paucity of data to indicate the number of salamanders per unit area in the southern Appalachian Mountains, we have calculated a density figure for the four most common species on the Yonahlossee Road (Table 2). We recognize that these data have inherent weaknesses. The figures do not represent the total number of salamanders per unit area, and do not represent crude density. Test & Bingham (1948), working with *P. cinereus* in Michigan, showed that the number of animals present on the surface (and *available* for capture) at any one time represents only a portion of the total population present in the area. The term *minimal* density is appropriate because (1) not every animal observed was captured; (2) a portion of the daytime sample was taken from the area collected at night; and (3) an estimate of the surface area covered in the daytime collecting was made. Two sets of figures are presented.
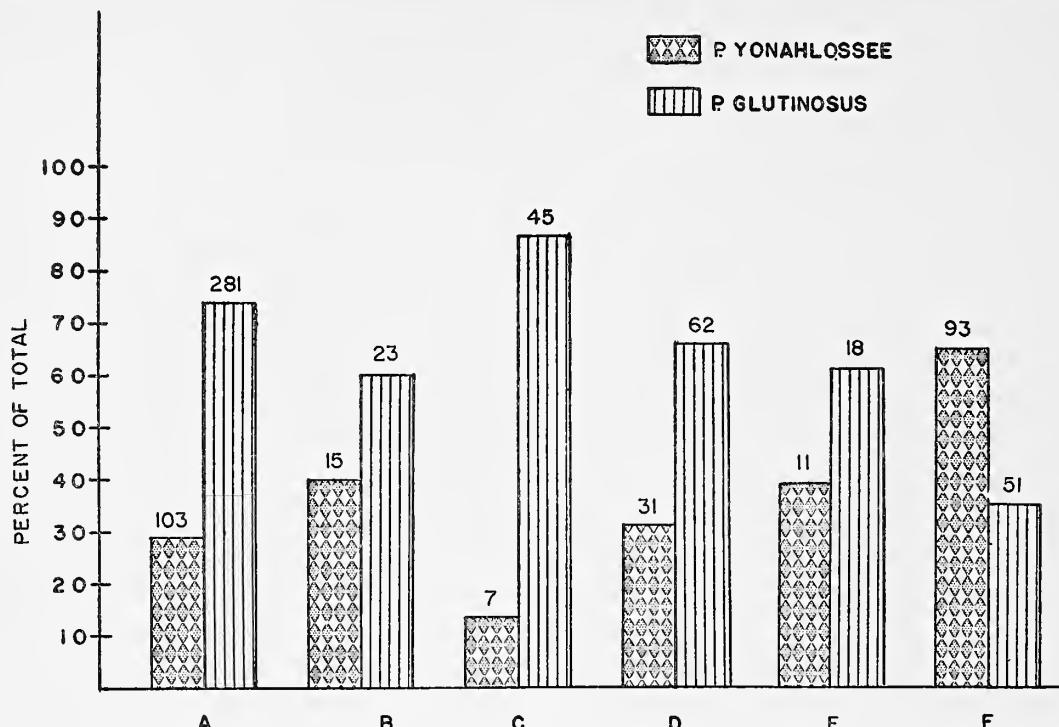
TEXT-FIG. 1. The relative abundance of *P. yonahlossee* and *P. glutinosus* at different localities and under different collecting conditions (**A**—Iron Mt., **B**—Buck Mt., **C**—Comers Rock, data from Pope, 1950; **D**—Linville 1917-20, day, data from Dunn; **E**—Linville 1960 day; and **F**—Linville 1960 night).

The data for the nocturnal sample were collected from a measured area (2.1 acres), but the sample is biased by the daytime collecting in the area. Those for the total sample were calculated from an estimated total area of 3.1 acres. Thus the figures represent minimal available densities and should be treated with caution.

We suggest that future collectors may find that sampling (even of the "one-stop" type) from a measured area will make their data on relative abundance more meaningful if the minimal available density is calculated for each species.

MICROHABITATS, BEHAVIOR AND COMPETITION

Pope (1950) points out that the existence of *P. glutinosus* and *P. jordani* at Linville "is of special interest and calls for further investigation in view of their ecological segregation elsewhere." His subsequent remarks (p. 87) imply that the sympatry of the two may be due to disturbed conditions brought about by lumbering. That this cannot be the case is evident from (1) Dunn's (1917) statement regarding ". . . the primitive condition of flora and fauna, and being rendered accessible by the splendid Yonahlossee

Road, is a paradise . . ." and (2) the existence of *P. glutinosus* and *P. jordani* together in the second-growth woods in approximately the same relative proportion today (1:5, respectively) as existed in Dunn's sample (1:3).

In view of the inability of competent taxonomists to distinguish between *P. glutinosus* and the southern representatives of *P. jordani*, we prefer to believe that a genetic difference in the two taxa which permits one to readily distinguish between them in the northern portion of the *P. jordani* range, also reinforces their ecological isolation where the two are sympatric.

TABLE 2. MINIMAL AVAILABLE DENSITY PER ACRE FOR THE FOUR MOST ABUNDANT SALAMANDERS ON THE YONAHLOSSEE ROAD, LINVILLE, NORTH CAROLINA

	Nocturnal Sample	Total Sample
Desmognathus ochrophaeus	56.7	70.0
P. glutinosus	15.7	16.5
P. yonahlossee	39.1	30.0
P. jordani	113.8	87.4

Pope (*op. cit.*) postulates competition between *P. yonahlossee* and *P. glutinosus* on the basis of similarity of "habitat niches" and food items. He was unable to demonstrate a convincing difference in diet. The fact that *P. glutinosus* is more readily available during the day than *P. yonahlossee* (as indicated by our collections and those of Dunn and Pope) leads us to think that there is a difference in microhabitat or behavior between the two taxa. Vernberg (1955) found that *P. glutinosus* was less photosensitive than *P. cinereus.* Our collections reveal an earlier peak of activity for *P. glutinosus* than for *P. cinereus* with *P. yonahlossee* intermediate. This seems to indicate that *P. glutinosus* is less light-sensitive than *P. yonahlossee.* *P. glutinosus* either (1) does not penetrate the subsurface to the depths inhabited by *P. yonahlossee,* or (2) takes advantage of its relatively less sensitivity to light and comes to the surface (beneath cover) during daylight hours more frequently than *P. yonahlossee.* In either case, *P. glutinosus* seems to be effectively isolated by microhabitat from *P. yonahlossee,* at least enough to reduce spatial competition. As long as an abundant food supply exists these two species can be considered only as potential and not actual competitors.

Concerning the habitat of *P. yonahlossee,* we are in essential agreement with Pope (1950) that this species is not "restricted to a zone within 100 feet" of streams as reported by Hairston (1949). The eastern margin of our plot was bounded by a stream, but there was no evidence that *P. yonahlossee* was any more abundant near the stream than it was toward the nettle patch on the western boundary.

Our observations of animals retained in the laboratory are of interest here. The animals were retained on wet leaves in large finger bowls with an excessive amount of moisture in the bottom. A series of pustules appeared on the skin of *P. yonahlossee* but not on the other plethodons retained in the same bowls. *P. yonahlossee* was observed more often on top of the leaves, than were the other taxa and this may represent moisture avoidance behavior.

ACTIVITY

Time was noted at intervals throughout the collecting period and determination of activity peaks of the various species was attempted. If peaks of abundance may be considered an index to peaks of activity (see Hairston, 1949), there is a suggestion that adults of the plethodon taxa are isolated during the active portion of the diel cycle on a temporal basis.

The young of all these species were especially prevalent before 9:00 P.M. Subsequent observations indicate that the young appear shortly after dusk and attain a peak of abundance by 8:00 P.M., 1 hour after sundown at this locality. Adults of *P. yonahlossee* attained a peak in abundance between 9:00 and 10:00 P.M., with a minor peak between 11:30-12:00 P.M. Between 10:00 and 11:00 P.M. both *P. yonahlossee* and *P. glutinosus* were often observed in refugia with only their heads exposed. *P. jordani* (juveniles and small adults) were present throughout the evening, but large adults (and *P. cinereus*) were definitely more abundant after 10:00 P.M. Although our sample of adult *P. glutinosus* was not large, we have the impression (at Linville and elsewhere) that the peak of activity outside the refugia is slightly earlier than that of *P. yonahlossee* (8-9:00 P.M.) These observations represent our concensus recorded immediately after the end of collecting. The observations were confirmed by one of us (JAM) who visited the area during August, 1961.

Our observations on behavior of the plethodons at Linville substantiate and supplement those of Dunn (1917) and Pope (1950). *Plethodon jordani* was observed on the leaf litter, near the bases of trees, logs and in open areas. Between 8:30 and 10:00 P.M., individuals seemed sluggish and were captured with the same ease as an individual found beneath a log during the day. However, from 10:00-12:00 P.M., this species became more active and agile and less easily caught. This latter behavior never approached that of *P. yonahlossee.* *P. jordani* climbs more often than the other three species of *Plethodon.* Many were collected on trunks and low branches of shrubs up to 3.5 feet from the ground. Groups were observed feeding on fungal gnats around decaying fungi, or on fruit flies and other insects at the base of trees from which sap flowed. *Plethodon glutinosus* was moderately abundant and easily caught in the early evening. No climbing was observed; practically all individuals were at the bases of plants, near logs or lying with their heads exposed in the openings of refugia. After 11:00 P.M., *P. glutinosus* was conspicuously absent from the surface area. This observation is not in accord with that of Hairston (1949), who reported an abundance peak at 11:00 P.M. in the Black Mountains during late July.

As described by Dunn and Pope, *P. yonahlossee* is the most agile of all eastern plethodons. Usually only one opportunity is available to capture an individual. If the collector misses, the animal retreats into a refugium for the evening. Numerous individuals were first seen with their heads sticking out of refugia. Others were moving at the bases of trees, or beside fallen rotted

logs and stumps. In most instances, this species was associated with a log over 10 inches in diameter, with not more than 1 to 3 inches of the log below the surface. A thick layer of leaf litter accumulation at the log–ground interface was a prerequisite. *P. yonahlossee* climbs more than *P. glutinosus* or *P. cinereus,* but less than *P. jordani.*

Summary

The type locality of *Plethodon yonahlossee* near Linville, Avery Co., North Carolina, was visited in August, 1960. The flora and physical aspects of two sampling areas, 2.1 acres and an estimated 1 acre, are described.

Diurnal collecting yielded 28.3 salamanders per man hour, as opposed to 46.8 salamanders per man hour at night. Ranking of the species according to percentage composition of the sample is shown to vary with the time in which the sample is taken.

The relative abundance of each species encountered is compared with Dunn's figures of 44 years ago. The most significant differences lie in a two-fold increase of *Desmognathus ochrophaeus* and a marked decrease in *Plethodon cinereus* and *P. jordani; Plethodon yonahlossee* and *P. glutinosus* have remained relatively constant.

The relation of *P. yonahlossee* to *P. glutinosus* is examined in terms of relative abundance in diurnal collections made by Pope (1950), Dunn (1917, 1920) and ourselves. Five localities are involved, yet the percentage distribution of the two species remains approximately the same at all but one locality. Competition between these two taxa, postulated by Pope (1950), is believed to be reduced by differences in microhabitat and behavior.

The minimal available density is calculated for the four most common species at the type locality. This density term is explained and its use as a quantitative basis for determination of relative abundance is suggested.

Temporal isolation in activity between age groups and the different species of *Plethodon* was observed and is discussed. General observations on behavior and microhabitat are offered.

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3

Sexual Discrimination and Sound Production in *Uca pugilator* Bosc

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(Plate I; Text-figures 1 & 2)

Introduction

THE purpose of this study was to investigate sexual discrimination and to describe certain display behavior, including sound production, by males of *Uca pugilator*. Specimens and models with various combinations of male and female appendages were introduced to resident males. Sound production was observed and the sounds produced were physically analyzed.

The reproductive behavior of fiddler crabs (*Uca* sp.) has been investigated by many workers during the last fifty years. In all species, copulation is usually preceded by display behavior, consisting of the "waving" of the male's large cheliped. In some species, sounds are produced which play a role in courtship. "Waving" behavior is believed to define the territory of the male and attract females (Crane, 1941).

Sound production in *Uca* involves movements of the large cheliped. Dembowski (1925) described a peculiar "shivering" of the large cheliped in *U. pugilator*, lasting from one to three seconds, which was used by one crab to "call" another out of its burrow. Crane (1941) reported sound production by "rapping" of the cheliped against the ground in three Pacific American species of *Uca*, and in *U. pugilator* (Crane, 1943). Burkenroad (1947) made observations on *U. pugilator*. He did not believe that rapping of the cheliped was involved in sound production in this species, as he failed to detect any disturbance of sand grains below the cheliped of a male that had just produced sounds. No rattling of the dactyl or vibration of the body could be detected. He concluded that some other mechanism of sound production was utilized. Rathbun (1914) described ridges, thought to be stridulatory, on the large cheliped

and ambulatory legs of male *U. musica*. Aurivillus (in Burkenroad, 1947) predicted, on morphological grounds, that stridulation would be found in the genus.

Burkenroad (1947) conducted experiments to investigate sexual discrimination in *Uca*. He released normal males, males without the large cheliped, and females of *U. pugilator* into an area occupied by resident males. In all cases, normal males evoked aggressive responses, but males without the large cheliped and females were courted by resident males. Altevogt (1957), working with *U. marionis* and *U. annulipes*, concluded that sexual discrimination by males was based on the presence of the large cheliped.

Materials and Methods

All observations and experiments were carried out on the west side of Pivers Island, Beaufort, North Carolina, during August, 1959 and 1961. The population of *U. pugilator* resided in clear areas of sand, either just above the high water mark or about 10 metres inland.

Sexual discrimination by males was investigated. In 1959, experiments were performed which repeated those of Burkenroad (1947). Males without the large cheliped, normal males, and females were released, in that sequence, and allowed to move through a 3 × 3 metre study area where over 40 males were exhibiting waving behavior. This sequence of releases was repeated ten times and the reactions of the resident males to all released specimens were recorded. In 1961, other introduction experiments were performed. A male that had previously exhibited waving behavior was frightened into its burrow. Two probes were placed in the sand about 0.6 metre to either side of the burrow

(Text-fig. 1). A dead specimen, killed by immersion in dilute alcohol, was placed between the probes. A long piece of thread was tied to a leg on either side of the body and then placed around one of the probes on the corresponding side and back about 1.5 metre toward the observer. The probes were placed in the sand so that by pulling the thread attached to either side of the dead crab, the specimen could be moved toward one or the other probe and within 7.5 cm. of the burrow. Dead specimens were introduced once to each of five resident males in this order: normal females; females with an attached large cheliped; normal males; and males with the large cheliped removed. Also introduced were two blue clay models of crab bodies. One model had two small chelipeds attached and the other, one large and one small cheliped attached to the anterior face. Each introduction consisted of slowly moving the dead crab or model from one probe to the other. After an experiment was completed, the male was frightened into his burrow. Another dead crab or model was prepared for the next test which was performed about five minutes after the male emerged from its burrow. Other introduction experiments were performed using live male
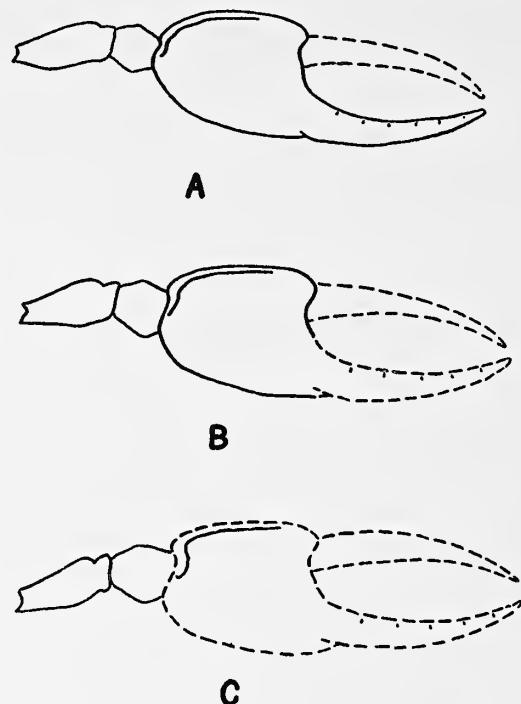
TEXT-FIG. 2. The appearance of the large cheliped of live male *U. pugilator* used in introduction experiments to conspecific resident males. In the first trial, the dactylopod was removed (A); in the second trial, the anterior half of the protopod (B); and in the third trial, the protopod was completely removed (C). The parts of the claw outlined with dashed lines represent the removed portions of the appendage.

specimens. These were also tied with thread and moved between the probes as described above. Before each introduction, portions of the large cheliped were removed (Text-fig. 2, A-C). For the first introduction, the dactylopod was removed; for the second, the anterior half of the protopod; and for the third, the entire protopod. All three introductions were performed once in the order described until each of five additional resident males had been tested.

Sounds produced by males of *U. pugilator* were recorded with a Magnecorder tape recorder (model PT63-A) and a Dukane microphone (model 7A150). The microphone was suspended above or placed on the sand 2.5 cm. from the burrow. The sounds were analyzed with a Kay Electric Company Sonograph Model Recorder (B).

RESULTS OF FIELD OBSERVATIONS

Resident males and females defended an area of 7.5 to 15 cm. in diameter around their bur-
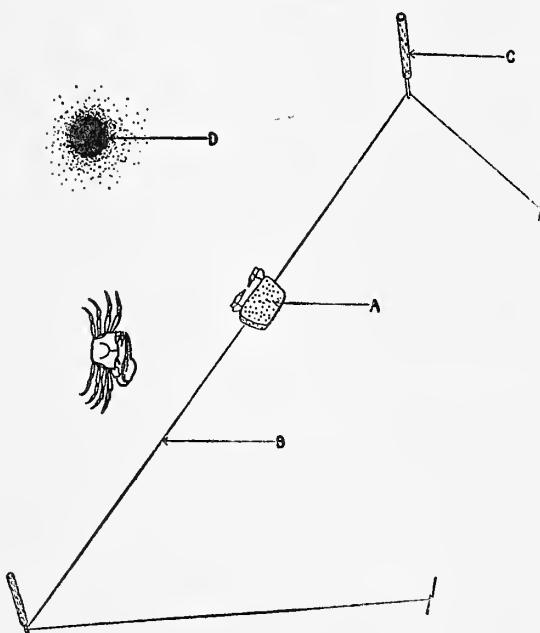
TEXT-FIG. 1. A clay model (A) with two small chelipeds attached is used to demonstrate the technique employed in introduction experiments. By pulling the thread (B) from either side, the model could be moved between the probes (C) and through the resident male's territory. The male's burrow (D) was about 7.5 cm. from the model when it passed through the male's territory..

rows from intruders of the same sex. Four resident females each approached by another female advanced with chelipeds extended and open. The intruder female then retreated from the area. More than five resident males approached by intruding males exhibited aggressive responses as follows. The resident male oriented so that the large cheliped was held slightly away from the body and with its broad surface facing the intruder. If the intruder came within 7.5 to 10 cm. of the resident male, the latter advanced, opening its cheliped, until the broad surfaces of both individuals' large chelipeds came into contact. The resident then pushed the intruder from its burrow, using its cheliped as a shield. Occasionally, the resident male pointed its opened claw toward the intruder. If the intruder advanced, the claws of both individuals would be locked together and the intruder was either pushed or flipped away by the resident. If the intruder was more aggressive, the resident male retreated into his burrow but with the large cheliped opened and facing upward out of the entrance. Intruding females either evoked aggressive or courtship behavior from resident males, the latter occurring more frequently. Observations by the authors confirm those made by Crane (1943) on the features of waving exhibited by males. The chelipeds were raised upward and, at the same time, the animal rose on its "toes." The claws were then extended laterally and lowered, as was the body. Finally, the chelipeds were returned to the anterior margin of the body. The frequency of the waving motion was about once every two seconds when no female was present. When a female approached, the frequency increased to more than twice that rate. The claw was not brought back to the body, but raised and lowered while laterally extended. The male oriented so that the broad face of the claw was turned to the female. If the female moved toward him, the male would go toward his burrow in short spurts of 2.5 to 5 cm., starting as the claw and body were raised and stopping as they were lowered. In five observations, the female followed about 5 cm. behind the male as he moved toward his burrow. The male then entered the burrow, but the large cheliped remained extended out of the entrance. Waving of the large claw continued, but when lowered it was vibrated against the sand at the lip of the hole, producing a rapid series of thumps. Similar sounds were heard after the female entered the male's burrow. On four occasions, lone males were observed making these sounds in their burrows at night by hitting the base of the large claw against the side of the burrow.

Over fifty sounds produced by one male in his burrow were recorded during the day. A sonographic analysis of three sounds is presented (Plate I). Each burst of sound had a duration of 0.2 to 0.3 seconds. Of the 17 bursts analyzed, 7 consisted of 5 pulses; 5 of 4 pulses; 3 of 3 pulses; and 2 of 6 pulses. Each pulse was produced when the claw hit the surface of the ground as it was vibrated. The sound energy was concentrated between 85 and 2,000 cycles. With sounds of higher intensities, a suggestion of harmonics was present with frequencies up to 10,000 cycles.

RESULTS OF INTRODUCTION EXPERIMENTS

The results of introduction experiments performed in 1959 were in agreement with those of Burkenroad (1947). Females and males without the large cheliped were courted, but normal males elicited aggressive responses from all resident males. Results of introduction experiments performed in 1961 are shown in Table 1. In all instances where dead crabs of either sex bore an intact large cheliped, the resident males responded aggressively. These responses were the same as those observed under natural conditions. When the dead introduced specimens bore no large cheliped, the resident males exhibited waving behavior and sound production typical of courtship. Neither waving nor aggressive responses were exhibited toward clay models with two small chelipeds attached. In two of five introductions, aggressive responses were exhibited to clay bodies bearing a large cheliped. Live male specimens with the dactylopod removed, and with the dactylopod and anterior half of the protopod removed, all evoked aggressive responses from resident males. Live males with the protopod removed were courted by four of five resident males.

DISCUSSION

Even though the specimens and models were not introduced to resident males in a random order, the following tentative conclusions can be made. Sexual discrimination in *U. pugilator* is based on the presence or absence of the large cheliped, regardless of the sex of the specimen bearing the appendage. This appendage releases aggressive behavior in male-male encounters, and may be important in inducing sexual receptivity in females. The posterior portion of the protopod, the broadest surface of the claw, is capable of eliciting aggressive responses from other males, so that an intact claw is not necessary for sexual discrimination.

The large cheliped also functions as a sound-producing organ and the sounds have come to

play an important role in courtship. Burkenroad (1947) suggested that sounds substituted for the attractive qualities of the large cheliped when that appendage could no longer be seen by the female. He found that sounds were produced more frequently at night than during the day. The results of our field observations seem to support this view. When a male produces sounds during the day, he is partially hidden from the female by the lip of the burrow so that waving motions of the claw could no longer be effective visual stimuli. The waving motion is then modified to include a rapid vibration of the claw against the ground. The sounds produced either substitute for the visual stimuli of waving or may have other functions in courtship.

The results of sonographic analysis as well as field observations support the conclusion that

stridulation is not used to produce sounds occurring during courtship in this species. A stridulatory sound is usually characterized by the concentration of the maximum energy in the higher frequencies. But rapid vibrations of the cheliped against the ground would be expected to produce thumping sounds which would show predominantly low frequency components such as those analyzed in this study.

SUMMARY

Courtship behavior of *Uca pugilator* was observed in a natural population. Waving behavior by males was exhibited when no female was present, but when a female approached a male, the waving motion was modified to produce sounds by vibrating the claw against the ground. A sonographic analysis of these sounds from one specimen showed that the energy of the sound was concentrated between 85 and 2,000 cycles and had a duration of 0.2 to 0.3 seconds. The role of sound production in the reproductive behavior of the species is discussed.

Sexual discrimination by males was studied by introducing models and specimens of either sex, bearing or not bearing the large cheliped (typical of male individuals), to resident males. In all cases, resident males exhibited aggressive responses to the specimens bearing the large cheliped and courted specimens without the large cheliped, regardless of the sex of the introduced specimen. It was concluded that the dominant visual cue in sexual discrimination was the presence or absence of the large cheliped.

TABLE 1. RESPONSES OF MALE *Uca pugilator* TO CONSPECIFIC MALES AND FEMALES AND TO CLAY MODELS[1]

	Number of Responses		
Stimulus	Waving	Aggressive Response	No Apparent Response
Dead Female	5	0	
Dead Female: large cheliped attached	0	5	
Dead Male	0	5	
Dead Male: large cheliped removed	5	0	
Clay Model: Two small chelipeds			5
Clay Model: one large, one small cheliped		2	3
Live Male: dactylopod removed	0	5	
Live Male: dactylopod and anterior half protopod removed	0	5	
Live Male: entire protopod removed	4	1	

[1] All tests with models and dead specimens were performed on the same five resident males. Live individuals were introduced to five other resident males.

ACKNOWLEDGEMENTS

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EXPLANATION OF THE PLATE

PLATE I

FIG. 1. Sonographic analysis of three sounds produced by one male *Uca pugilator* in its burrow during the day.
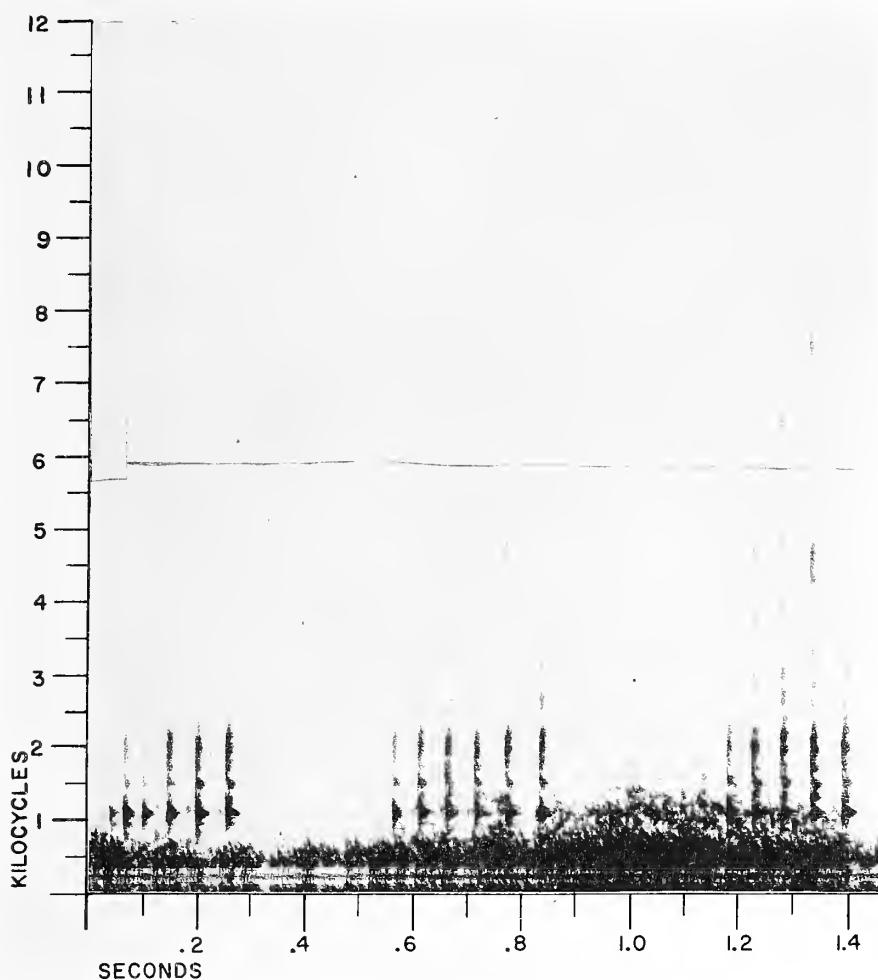
FIG. 1

SEXUAL DISCRIMINATION AND SOUND PRODUCTION
IN UCA PUGILATOR BOSC

4

Low Temperature Effect on the Testicular Cell-components of the Common Indian Toad, *Bufo melanostictus* Schneider

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(Plate I; Text-figure 1)

THE degree of warmth, humidity, light and other climatic features in combination with the internal rhythm are responsible for controlling the sexual pattern of animals. The environmental temperature plays a great role in the reproductive physiology of poikilothermous animals such as fishes, amphibians and reptiles, although this appears to be lacking in warm-blooded birds and mammals (Bullough, 1951, p. 29). The potentially continuous type of spermatogenesis of *Rana esculenta* could be suppressed by decreasing the temperature during summer time, and the reverse during the winter induced activity (Galgano, 1934, 1935). Similar action on spermatogenesis was also proved to be true when *Triturus cristatus cranifer* (Galgano & Falchatti, 1940; Mazzi & Galgano, 1949), *Triturus viridescens* (Ifft, 1942), *Geotriton fuscus, Triturus alpestris, Rana gracea* and *Rana latestei* (Cei, 1942 a, b, and 1944) were treated with high temperature during winter and summer months. In the South American wood frog, *Leptodactylus ocellatus typica,* Cei (1948) and Rengel (1950) observed a temperature tolerance limit both in summer and winter and spermatogenesis is reported to be impaired if the frogs are treated beyond that range in both the seasons. However, Rengel (1950) was unable to observe any such effect when *Leptodactylus ocellatus reticulatus* was treated at high tempearture (± 30°C). Similarly, Cei (1944) could not induce spermatogenesis in *Rana arvalis* when it was treated with high temperatures during winter. Witschi (1924) reported that spermatogenesis is independent of environmental temperature in *Rana temporaria.* This was experimentally supported by Cei (1942, 1944) by keeping the frogs at high temperatures during the winter. But van Oordt (1956a, b)

treated *Rana temporaria* at 5°C for two months and observed the absence of spermatogenetic activities. In *Telmatobius schreiteri* (Cei, 1949) and *Hyla raddiana andina* (Caruso, 1949) spermatogenesis is continuous and is not affected by the considerable low temperature of the high altitudes of the Andes mountains.

It is, therefore, evident that spermatogensis is dependent on the temperature in most of the Salientia, but with some specific variations. The above reports are from the temperate zone with the exception of some South American tropical examples. Consequently, it appears useful to study the influence of low temperature especially on tropical toads like *Bufo melanostictus* where spermatogenesis is continuous (Mondal & Basu, 1960; G. Church, 1960) and is not affected by an average temperature fluctuation of 38°-15°C.

MATERIALS AND METHODS

Mature male toads, *Bufo melanostictus*, were collected from the vicinity of Calcutta and were brought to the laboratory the next day. The body weight and snout-to-vent length of all experimental animals varied from 28-32 gms. and 70-75 mm. respectively. Secondary sexual characters were carefully observed before treatment. A group of ten toads was allowed to stay in a controlled temperature room (±10°-15°) and another batch of five was kept at outside normal room temperature for one month. This experiment was performed during the months of August-September 1960 (Group A) and April-May 1961 (Group B). At the time of autopsy, body weight, snout-to-vent length, testicular weight and secondary sex characters were noted. The right testis of all the individuals was fixed and sectioned at 6μ and stained with hematoxylin

TABLE 1. OBSERVATIONS TAKEN FROM THE CONTROL AND LOW TEMPERATURE TREATED TOADS FOR THIRTY DAYS DURING THE MONTHS OF AUGUST-SEPTEMBER (1960) AND APRIL-MAY (1961).

| | Relative Testis Wt. (in mg.) | Testis Tubule Diameter (in μ) | Spermatogenetic Stages‡ | | | | | | Percentage of Tissue Components | | |
			0	I	II	III	IV	V	Interstitium	Testis Tubule	Misc.†
August-September (1960) Group A											
Control (5)*	70	52.5	47.0	26.0	40.5	75.5	4.0	5.2	10.8	87.5	1.7
Treated (10)* ±10°-15°C 30 days.	67	45.5	48.2	25.0	42.5	70.5	2.7	4.0	20.35	78.6	1.15
April-May (1961) Group B											
Control (5)*	134	57.0	35.0	23.0	40.5	80.2	2.0	3.2	17.5	81.2	1.3
(Treated) (10)* ±10°-15°C 30 days.	135	56.5	37.0	22.5	27.5	75.7	2.2	4.0	18.2	80.5	2.3

*Figures indicate the number of toads used. †Includes blood vessels, vasa efferentia and some empty spaces. ‡Stage O = Primary spermatogonia at resting phase. Stage I = Secondary spermatogonia less than ten cells in a cell nest. Stage II = Secondary spermatogonia more than ten cells in a cell nest. Stage III = Primary spermatocyte. Stage IV = Secondary spermatocytes. Stage V = Spermatids.

eosin. Different spermatogenetic stages were counted and the percentage of tissue components was calculated by a planimetric method. Tubule diameter and relative testicular weight were also recorded.

RESULTS AND DISCUSSION

The relative testicular weight of both control and treated toads of Group A (*vide* Table 1) is well within the normal range, as was previously reported by Mondal & Basu (1960) in dealing with the annual spermatogenetic cycle of the present species. The overall picture of the different spermatogenetic stages and the average number show no distinct difference caused by the treatment. A decrease, although not very remarkable, in the number of cell nests from stage III onward is observed among the treated toads of Group A (August-September, 1960). Sperms are embedded in the Sertoli cells and the vasa efferentia remain closed in all the treated and control toads during the months of August-September, 1960. The most prominent difference is noted in the testis tubule diameter, which is definitely narrow in the treated group (45.5μ) when compared with the controls (52.5μ). Similarly the percentage of interstitium has increased in the treated batch of animals (20.3%) as compared with that of the controls (10.8%). About 10% increase of the interstitial cellular components due to low temperature and an average shrinkage of 7μ of the tubule diameter are definitely significant (Text-fig. 1; Plate I, A & B).

In toads of Group B (April-May, 1961) both control and treated individuals show differences of insignificant nature in their relative testis weight, tubule diameter and also in their percentage of tissue components (Table I; Text-fig. 1). So far as the different spermatogenetic stages are concerned, an abrupt and sudden fall in the cell nest number of the secondary spermatogonia of stage II is noted in the treated group. The number of spermatocytes has also been decreased but not as significantly as have the spermatogonia. The sperms are found both in scattered and bundled condition in the tubular lumen, suggesting spermiating activity in the toads (Plate I, C & D).

The experiments of Galgano (1934, 1935) on *Rana esculenta* proved beyond doubt that temperature can induce or suppress spermatogenesis. On the other hand, in *Rana temporaria* Witschi (1924) and Cei (1942, 1944) believed that temperature caused no significant influence on spermatogenesis. Later, van Oordt (1956 a, b) and Galgano & Lanza (1951) proved that the influence of temperature exists in *Rana temporaria* if treated for a long period. All the above-mentioned observations are limited to the frogs of the temperate zone where normal environmental temperature is very low. On the contrary the frogs and toads inhabiting the tropical and subtropical zones generally show a continuous type of spermatogenesis and their temperature tolerance limit is also variable. This appears to be inherent and varies from species to species.
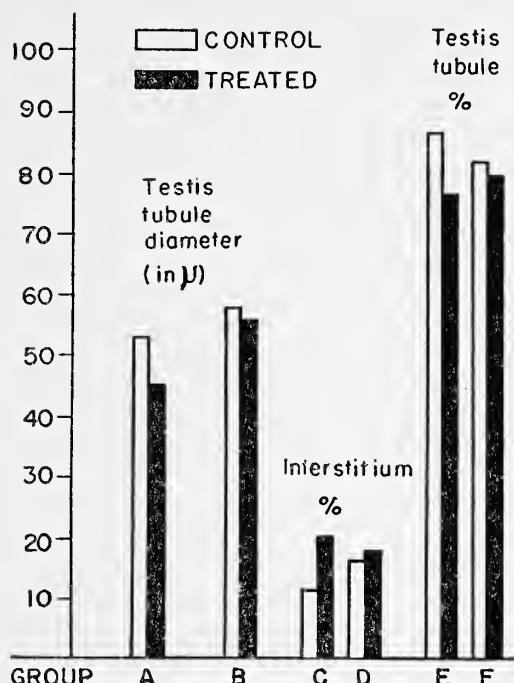
Text-fig. 1. Illustrating the change in the tubule diameter (in μ), interstitium percentage and testis tubule percentage of control and treated toads in Groups A, C & E (August-September) and Groups B, D & F (April-May).

The normal cycle of *Rana tigrina* (Basu & Mondal, 1961) and *Bufo melanostictus* (Mondal & Basu, 1960; Church, 1960), inhabiting more or less the same climatic zone, show a good deal of difference particularly during the winter months. A similar condition is reported by Rengel (1950) with regard to a South American species of *Leptodactylus,* which shows continuous spermatogenesis. Rengel (1950) observed that if *Leptodactylus ocellatus reticulatus* is exposed to temperature higher than ±30°C there is no harmful effect on spermatogenesis, but this temperature appeared to be too high for the testicular cell divisions of *Leptodactylus ocellatus typica.* The present experiment on *Bufo melanostictus* reveals that very low temperature treatment in the warmest days (±36°-40°C) of the year (April-May, 1961) causes no significant effect except the decrease of the secondary spermatogonial number. But the toads of Group A (August-September, 1960) under similar treatment did not show any such remarkable fall in the cell nest number of stage II. On the contrary the tubule diameter and percentage of the interstitium was remarkably affected by low temperature in Group A. This proves that the role of low temperatures on male gonads of

Bufo melanostictus is different during the summer and autumn months. In summer probably the spermatogenetic stages are more susceptible than is the interstitium of autumn. However, it is expected that prolonged treatment for several months may affect all the target organs during the summer and autumn months. In *Rana temporaria,* Witschi (1924) concluded that spermatogenesisis is to a large extent independent of the environmental factors and consequently depends on the internal rhythm determined by genetic factors. But experiments of van Oordt (1956) suggest that prolonged treatment may change the condition. Cei (1948) and Rengel (1950), from their experimental observations, are of the opinion that there remains a certain temperature tolerance limit in the spermatogenetic field of the Salientia. Moreover, from different reports so far available it appears that the temperature tolerance range of the Salientia varies from species to species even in the same climatic zone. The present experiment also suggests that in *Bufo melanostictus* seasonal variation causes some difference in the site of sensitivity and also that it has a wide range of temperature tolerance which is suitable for its adaptation to this tropical climate.

Summary

1. The common Indian toad, *Bufo melanostictus* Schneider, was treated with low temperature (±10°-15°C) during summer (April-May) and autumn (August-September) months of the year. The treatment was continued for one month.

2. No significant effect on spermatogenesis was observed except a sudden fall in the number of secondary spermatogonial cell nests of treated toads during the summer season.

3. The autumn toads after treatment showed a decrease in the diameter of the tubules and an increase in the percentage of interstitium in the testis tissue components.

4. Possible significance of the changes due to this treatment and some probable explanations have also been discussed.

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EXPLANATION OF THE PLATE

PLATE I

(Photomicrographs of 6μ sections through the testis of *Bufo melanostictus*)

A. Section showing the hyperplasia of the interstitium (*vide* arrow) and narrow tubule diameter of treated toads during August-September (Group A). × 100.

B. Section showing the normal condition of the testis in the control toads of August-September (Group A). Note the undifferentiated interstitium and wide tubule diameter. × 100.

C. Testis sections of treated toads during April-May (Group B), showing the sudden fall of secondary spermatogonia (Stage II) in the follicles. × 100.

D. Section through the testis of control toads of Group B showing very little difference except the normal number of secondary spermatogonia (arrow indicates the stage II cell-nests). × 100.
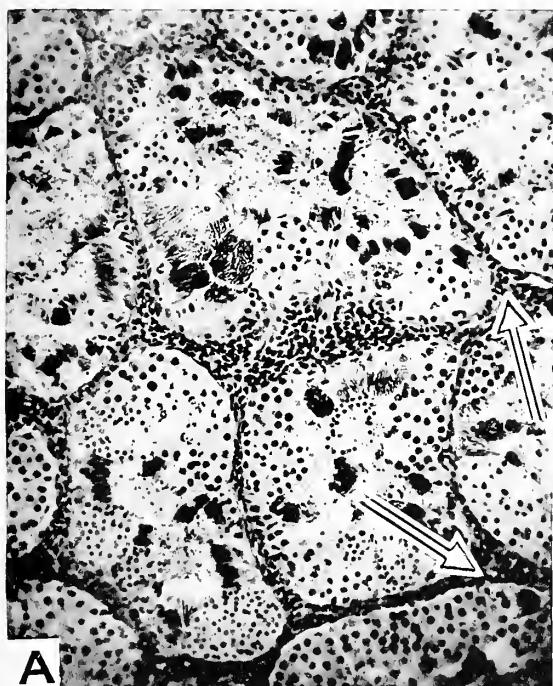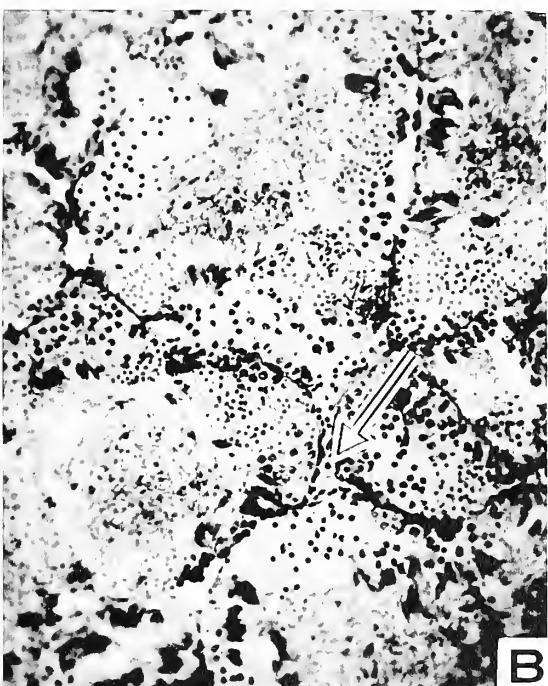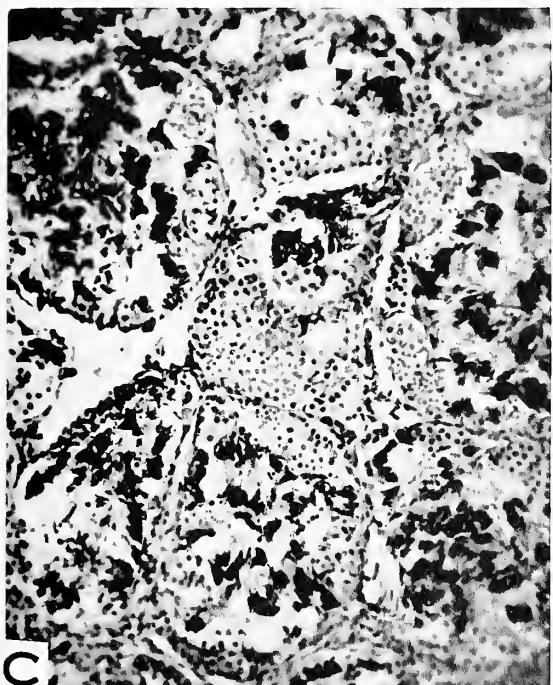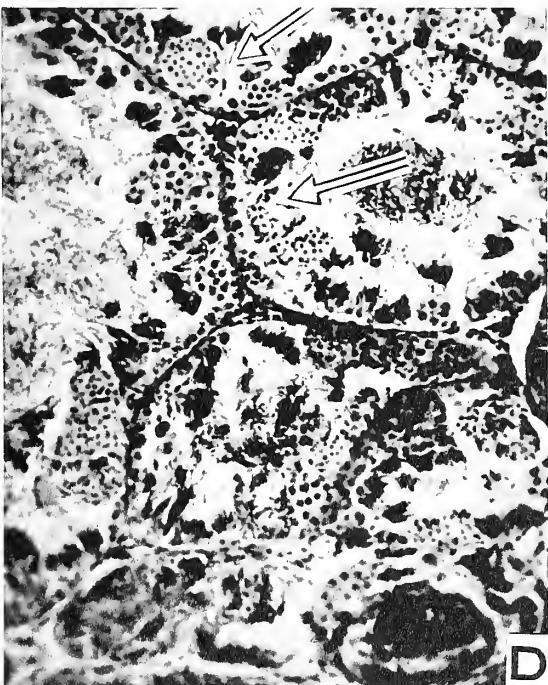
PLATE I

LOW TEMPERATURE EFFECT ON THE TESTICULAR CELL COMPONENTS
OF THE COMMON INDIAN TOAD, BUFO MELANOSTICTUS SCHNEIDER

5

Biology and Behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, W.I. (Arachnida, Pedipalpi)[1]

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(Text-figures 1-5)

Contents

Introduction

TAILLESS whip-scorpions or scorpion-spiders are dorsally flattened, cryptically colored arachnids, found in tropical and sub-tropical regions. Their systematic position is controversial so that a study of their biology and behavior is not only interesting in its own right, but might also be relevant to this question. The scorpion-spiders have traditionally been placed in the arachnid order Pedipalpi, but in 1949 Millot replaced this by two new orders, the Uropygi and the Amblypygi, the latter containing the scorpion-spiders. Subsequently Petrunkevitch (1955) has divided the Pedipalpi into three separate orders, the Thelyphonida (true whip-scorpions), the Schizomida and the Phrynichida (scorpion-spiders). He agrees with Millot, however, that the first two are more closely related to each other than either are to the scorpion-spiders. Both of these proposals imply that the previous order Pedipalpi reflected similarities which had in fact arisen in two separate lines of evolution. All these conclusions have been reached from a consideration of the morphology of the animals, the more recent suggestions taking into account the internal as well as external features. It seemed possible that behavioral characteristics might supply evidence for or against the suggested convergence of the Schizomida and Thelyphonida with the Phrynichida. Few records have been made of the behavior of the Pedipalpi as a whole and this dearth of information is especially noticeable in the case of the Phrynichida. The present observations on *Admetus barbadensis* and *Damon variegatus,* both members of the family Tarantulidae, are offered in view of this lack. It is hoped that if they serve no other purpose, they may provide some incentive to record the equivalent information for the other two groups; for until comparative studies have been made on the animals as a whole, much of what is said here must remain a speculative contribution to the subject of pedipalp relationships.

Habitat

In the field these scorpion-spiders can be found beneath loose pieces of wood or leaves, more especially under forest cover. There is no indication that they ever construct burrows for themselves either in the wild or in the laboratory, as has also been reported by Gravely (1915) for the East Indian scorpion-spiders. If the cover is suddenly removed from a specimen, it may stay absolutely still, presumably employing behavior

which would sometimes lead to its being over-looked because of its general flatness and cryptic coloration. If it moves, it does so quickly, running suddenly sideways onto another surface of the covering object or away to another hiding place. It never threatens unless it has actually been picked up and then only occasionally.

D. variegatus is more markedly synanthropic than *A. barbadensis* and in many parts of Natal can be collected very readily from cellars, out-houses or man-holes where it lives either in crevices or freely on the walls if the place is fairly dark. This acceptance of human habitation is a biological feature which contrasts with the behavior of the schizomids and thelyphonids, neither of which has been reported to occur associated with man.

In laboratory conditions both *A. barbadensis* and *D. variegatus* show a diurnal rhythm of activity in which the active phase is nocturnal and since the former species has been found wandering about at night in the forests of Trinidad, it is assumed that the activity pattern shown in the laboratory is a natural one and not induced by disturbances during the day. Similar habits occur in the other two groups but it is common for most arachnids to be nocturnal.

FEEDING

There is no information about what the scorpion-spiders eat in the field. Prey is, however, caught at night and is almost certainly living. Animals such as moths, crickets, spiders, cockroaches and beetles are accepted in the laboratory and probably form part of the normal diet. In stalking prey, the scorpion-spider approaches directly, *i.e.*, not sideways as in escape. The tips of the first pair of legs[3] tap the prey so gently that they seldom disturb it. When the scorpion-spider is an inch or two from its prey, it suddenly throws itself upon the insect, clutching at it with the exposed spines of both pedipalps. Sometimes, when the prey is especially large, the scorpion-spider attacks several times in this manner, retreating between each attack. More usually the insect is impaled on the pedipalpal spines at the first onslaught. Once the prey is caught, the pedipalps fold, pulling it towards the mouth and retaining their hold of it while the needle-like chelicerae alternately dig down into it.

After the meal the corpse is often left as a mangled mass of exoskeleton but this is not invariably so; sometimes it remains almost entire,

only showing external damage at the points where the chelicerae had punctured it. This is strongly reminiscent of what occurs among the spiders and suggests that scorpion-spiders may also rely on extra-oral digestion to a considerable extent.

Such a consideration leads directly to the problem of how the food is conveyed into the gut, once it has been liquified by the digestive juices. Just behind the mouth opening there is a typically arachnid sucking pharynx and ingestion itself consists of drawing up the fluid contents of the corpse into this sac.

Both scorpions and scorpion-spiders possess "pseudotracheal" areas on certain limbs. In the scorpions such filter-like areas are located on the coxal endites of the second legs. During feeding either digestive juices pass through these and onto the food or the liquified food passes through them into the gut: there is no decisive evidence as yet to distinguish between these possibilities. Limb movements, which occur during feeding, could help move the fluid in either direction. In the scorpion-spiders there is no limb movement, yet on each coxa of the pedipalps they have a pseudotracheal area structurally resembling the pseudotracheae of a scorpion. The main channel, like that in the scorpions, opens into the base of the esophagus.

In captivity scorpion-spiders frequently drink water. In this behavior, as in the eating pattern, there are alternate movements of the chelicerae. These cease for short intervals as fluid is drawn up into the gut. The significance of the cheliceral movements is obscure; perhaps they are merely a reflection of the fact that the animal uses the motor pattern of normal feeding when drinking free water. Conversely, the similarity of the eating and drinking patterns is in keeping with the suggestion that it is a fluid which is taken up into the mouth during feeding and that extra-oral digestion must occur.

As with the detection of prey, the detection of water appears to be done by sense organs on the feelers. This may be demonstrated as follows: A desiccated animal is put on the bottom of a dish which has a number of small holes bored in its lid and many drops of water placed between these holes. During its investigation of the dish, the scorpion-spider will eventually put one of its feelers up through a hole and into a drop of water. Immediately, the behavior pattern of drinking can be seen in the animal below and it will make efforts to get at the water. The sense organs involved have not yet been identified, nor is it clear whether the feelers only can be used for detecting water.

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[3] The first legs are very long and antenniform and will be referred to throughout this study as the "feelers;" see Patten (1917).

WASHING

This behavior may be seen most frequently after the animals have been drinking or eating, though they will interrupt other behavior, such as courting or fighting, to wash themselves. The feelers and walking legs are pulled to the mouth by the pedipalps and then drawn between the chelicerae, being cleaned by the medial brushes which occur on these appendages (Text-fig. 1a). During washing, the chelicerae move up and down as they do in eating or drinking.
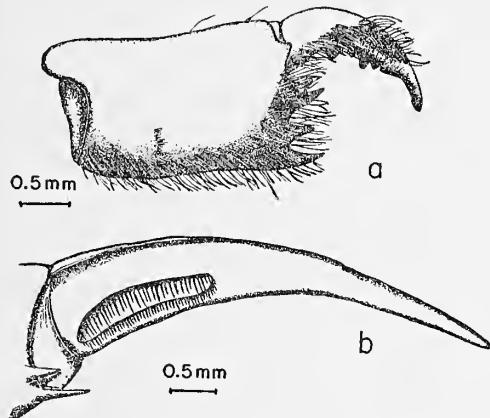
TEXT-FIG. 1. **a**—Lateral view of the left chelicera of *A. barbadensis*, showing the mesial brushes on both first and second segments. **b**—Lateral view of the last segment of the pedipalp of *A. barbadensis*, showing the structure used by the animal for washing its limbs.

The catching of a leg or feeler by the pedipalp may occur as a preliminary to its being washed between the chelicerae, as described above, but the action may also be repeated over and over again without the chelicerae being involved at all; the limb is pulled a short distance towards the mouth by the pedipalp and then released. Here the pedipalp itself is doing the cleaning: the apparatus concerned is a little close-haired brush on the last segment (Text-fig. 1b)[4]. The limb is drawn through this brush as it returns to its position after being pulled towards the mouth. The important function of the cleaning brush, however, is the washing of the pedipalps themselves. Though the brushes of the chelicerae are able to clean some of the spines on the inner surface of the pedipalp, this cleaning action is incomplete and many of the pedipalpal spines

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[4] It is this structure that Barnard, *Ann. Mag. nat. hist.* (6), 11, 28-30 (1893), suggested was a sense organ, and the homologue of the adhesive organ on the last segment of the pedipalp of the solifugid.

are not reached at all. If the pedipalpal spines are to act as weapons, their sharpness is all-important. This must depend on their being kept free of congealed remnants of prey and dirt and it is desirable that there should be a mechanism for cleaning them properly. It is the pedipalpal brushes which do the major part of this cleaning, wiping each of the large spines in turn, then cleaning the outer surface of the pedipalp itself. The brushes are themselves cleaned on the cheliceral hairs, these being moistened at the mouth. It seems possible that the brush on the pedipalp of *D. variegatus* and *A. barbadensis* has been evolved primarily for the cleaning of these pedipalpal spines. Millot (1949) shows the presence of the brush in his illustration of *Charinus milloti* Fage, a member of the Charontidae, the second family of Phrynichida. So pedipalpal brushes may occur throughout the whole order; possibly they were one of the prerequisites for the capitalization of the pedipalpal spines as weapons.

INTRASPECIFIC BEHAVIOR

Aggressive and threatening behavior occurs in encounters between two males or two females, between an adult and a young animal or even between two young animals, and the same behavior comprises the first part of courtship in any pair of scorpion-spiders. Hence a description of actual courtship behavior will be left until after consideration of intraspecific behavior which does not lead up to mating.

In an encounter between individuals that are clearly unevenly matched, (*i.e.*, a small and a large individual or one injured and one intact), regardless of which touches the other first, the result is almost always the same. The "inferior" animal runs off sideways for a short distance and then extends the nearer feeler towards the superior animal, quivering it violently in the air over the body of the other. Then, without necessarily any further move from its antagonist, the weaker will suddenly fold in its feelers and run off as far as possible from the other. Sometimes the superior animal may unfold its pedipalps and threaten or even rush and fling itself at the inferior. Invariably, however, the latter animal escapes uninjured from the first encounter. In laboratory observations it may subsequently be killed, but such an event should perhaps be regarded as something that would not normally occur in the field; it seems to happen only when the weaker animal is allowed no space for escape.

When the contestants are more evenly matched, the first encounter may, as in the previous case, include violent pedipalpal attack. Here the two animals will strike at each other

with one or both pedipalps. The spines on these appendages may tear the carapace or abdominal tergites or rip open the swollen intersegmental membranes of the pedipalps where they are exposed in threatening. Such wounds are often fatal and, if the stricken animal is not eaten immediately by its opponent, it will usually be dead by the following day.

In addition to these direct attacks, however, there are numerous conflicts that end without any blood being shed. Such encounters may be described as threat fights and they precede almost all true courtship. There are several variations, but in general the victor must beat its opponent into submission using only its delicate feelers. Although the blows may be given with such force that the body of the opponent sways beneath them, it is obvious that little discomfort, let alone hurt, could come from them. This would appear to be a case of highly ritualized threatening which does not involve the weapons of offence themselves.

The commonest form of threatening is what is here called "side-tapping." The animal concerned faces about 45° away from its opponent, (Text-fig. 2a), bends its abdomen so that it is more nearly in line with the opponent, extends and opens the pedipalp furthest from the enemy and taps or beats the latter's body with the nearer feeler, which is stretched out in front. The body of the animal doing the tapping is nearly always held very close to the ground, as if it needs support.

The opponent normally does one of two things: either it returns the tapping, using precisely the same pose as does the first animal so that a very symmetrical effect is achieved (Text fig. 2b) or it stands up, holds its body well away from the ground and allows the first to beat at it (Text-fig. 2c). If the latter response is made, the animal which is being beaten usually extends its pedipalps to some extent, drawing the tips fairly close together and keeping the claws (formed by the spines) closed, *i.e.,* not using the normal threat pose in which the pedipalps are both extended and opened.

Whether there is mutual side-tapping or whether only one animal taps, the behavior lasts

TEXT-FIG. 2. Diagrammatic representation of an encounter between two specimens of *D. variegatus.* Animal I is above, with its feelers represented in black, Animal II is below and is the smaller. In all cases the full length of the feeler of Animal I is not shown in proportion to its body. a—Animal I is side-tapping, leading with the left feeler while the right is folded back. b—Animal I is side-tapping slightly more actively, as can be seen from the fact that its body is more fully oriented towards II and it has opened and extended its right pedipalp further. Animal II is now returning the side-tapping so that there is a mutual exchange of blows. c—Animal I has gone into what is virtually the extreme side-tapping pose while II has taken up the "passive" stance, with legs raising the body high above the substratum while the pedipalps are half extended and the claws almost completely closed. The feelers curve forward gently and touch at II.

only a short time and then there is a reorganization. In the case of mutual side-tapping, the pair pull in their feelers and face each other. Then they gradually revert to side-tapping once more but this time leading with the other feeler. Before the new orientation and as the animals face each other, the feelers may exchange a few beats. Occasionally, after coming forward to change, the pair revert to leading with the same feeler as they were using before. Less frequently, one animal will change its leading feeler while the other will not, thus producing a thoroughly disorganized side-tapping.

If only one animal of the pair has been tapping, and the other is passive, the roles are reversed periodically; thus the passive scorpion-spider begins to tap while its partner rises up on its legs, brings both pedipalps to the half-extended position and holds its feelers partly back, *i.e.*, it assumes the passive role.

Another behavior pattern can be distinguished; this seems to occur in animals which are both more active than the couples described above. Each stands with its pedipalps open and partly, or even widely extended and then the animals lunge in turn towards each other. Sometimes they spike the body or one of the limbs but quite frequently they miss altogether. Sometimes both animals strike together and the spines of the two pairs of pedipalps become entangled. A slight variation of this pattern is one in which both animals move sideways, facing each other and occasionally lunging across the space that separates them. In some cases the same dance-like steps occur but the animals merely beat at each other with their feelers instead of using their more offensive pedipalps.

These various patterns may merge into one another or change abruptly from one to the other; there is as yet no clear explanation of the significance of each, or of why or how the changes are initiated. The sequence does not seem to have any precise bearing on the final result of the encounter. This latter takes one of three forms. Firstly, there may be a serious pedipalpal exchange between the pair and in this one or both may be injured or killed. Secondly, one of the pair may suddenly turn and run off rapidly (behavior that does not normally follow a series of active tapping at the opponent). Lastly, one or both of the animals may just wander off slowly and pay no further attention to the other.

COURTSHIP

True courtship is far more difficult to observe than the encounters recorded so far. The chances of seeing this behavior, however, are increased if the observations are made at night and under a very dim or red light. In neither *D. variegatus* nor *A. barbadensis* can the sexes be distinguished from a glance at the dorsal surface and so, for experimental work, it is convenient to determine the sex of each animal and mark its back with appropriate paint. Sexing can be done using the differences in the details of the furrows on the genital operculum, as was suggested for *D. variegatus* by Lawrence (1949). With live animals, however, it is better to hold the animal on its back and lift the edge of its operculum gently; if it is a male, the genital organs will be extruded (Text-fig. 3a). These male organs will be referred to here as "genital cones." (The term "penes" used by Lawrence (1949) is unacceptable for, as will be seen later, they do not function as intromittent organs). They are relatively larger in *A. barbadensis* than in *D. variegatus* and consist of a pair of conical structures (Text-fig. 3b) almost joined together at their bases, each opening towards the midline by way of many peculiar foldings. The male ducts lead into the bases of these genital cones.

The under surface of the female operculum bears no such organs, but in the female *A. barbadensis* there is a pair of small dark-colored sclerites lying obliquely just under the operculum (Text-fig. 3c). These point towards the midline and are attached anteriorly. Their function will be discussed later in relation to the egg-case. The female *D. variegatus* lacks these sclerites and has instead a number of complicated foldings of the cuticle, some of which are sclerotized (Text-fig. 3d). In either case the single opening of the female duct lies at the base of the operculum.

Returning to the actual courtship, it has already been said that this is normally preceded by certain behavior patterns which also occur in encounters between animals of the same sex or immature stages. In the first part of an encounter the degree of violence may vary widely, but eventually, if genuine courtship is to follow, the animals will reach a stage when the female response to the side-tapping of the male becomes one of submission. Instead of holding her body stiffly away from the ground, she allows it to come to rest, spreading her legs out sideways. Her pedipalps are folded from the semi-extended position into one of rest and her feelers become motionless. The male then straightens his body and comes forward to face her; he beats her intermittently with both feelers. Presently he extends his pedipalps fairly slowly and lunges at her, pushing her with his body as if testing her passivity. During these advances, the female may show signs of recurring aggression and immediately the male will move back and again
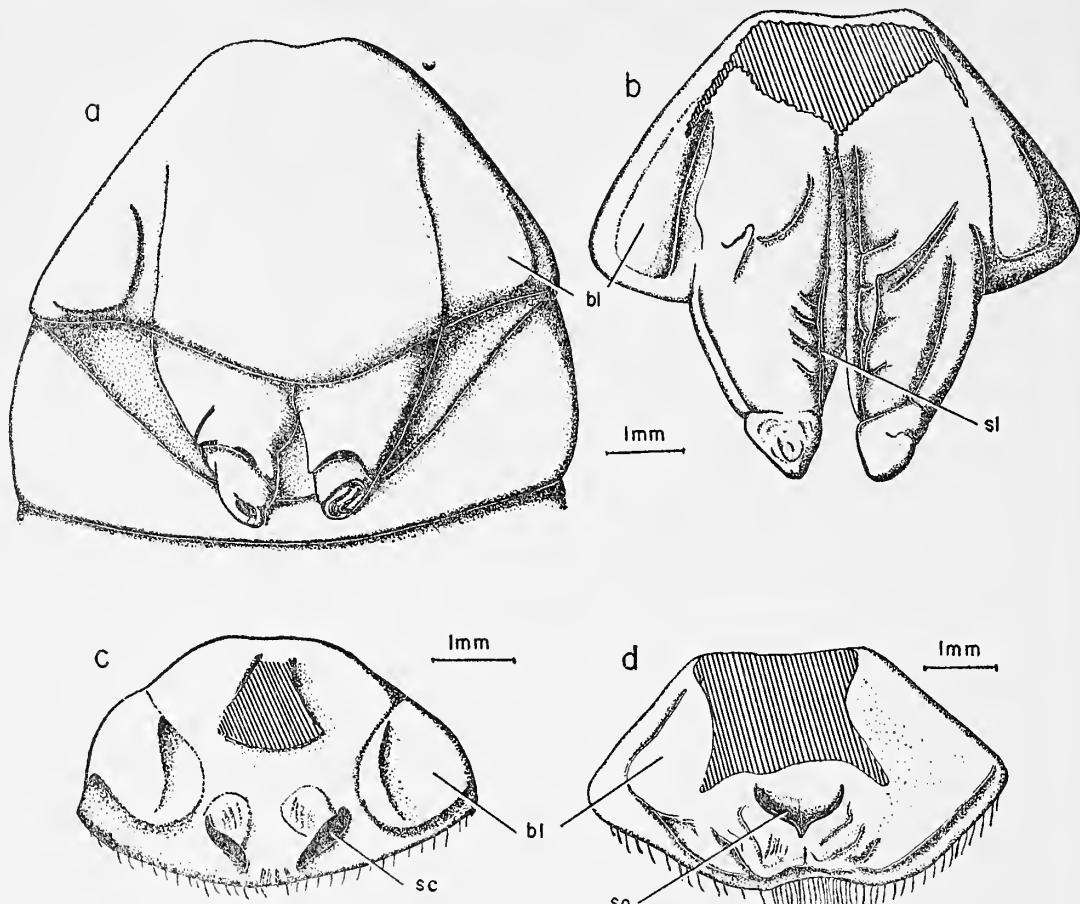
TEXT-FIG. 3. **a**—Genital area of *A. barbadensis* showing the extruded genital cones. **b**—View of the genital cones from the undersurface of the genital operculum The male ducts and accessory glands would empty into the cones through that part which is shown by cross-hatching in the diagram. Part of the slit-like opening of the cones can be seen, **sl**. **c**—Undersurface of the genital operculum of a female *A. barbadensis* to show the sclerites, **sc,** which hold the anterior end of the egg-case. **d**—Undersurface of the genital operculum of a female *D. variegatus* showing the foldings and sclerotization which occur there in the formation of a socket, **so,** into which the anterior end of the egg-case is moulded. The position of the first pair of book-lungs can be seen, **bl**.

begin his intermittent beating. Such upsets occur more and more infrequently until, eventually, after some hours, she lies passively under all his advances.

D. variegatus completed courtship in the laboratory on one occasion only and then a part of the behavior was not seen. Courtship climaxed by mating has, however, been watched in *A. barbadensis* on five occasions. The patterns of courtship and mating were virtually identical—except for points of difference introduced by deliberate interference. It seems likely that the behavior in the two species is the same.

There is no mating grasp at all in these scorpion-spiders and the animals remain un-connected throughout as in some of the pseudo-scorpions and mites.

Once the female is truly passive, mating can begin. The male lowers his body and touches it to the ground several times. He gets up, moving closer to and almost touching the body of the female who remains motionless. He turns round so that he faces directly away from her and, lowering his body, crouches down on the substratum as before. A slender, transparent spermatophore is then extruded from his genital opening. Once the distal end of the spermatophore is cemented onto the ground, the male scorpion-spider raises himself and turns round so that he again faces the female. He then moves for-
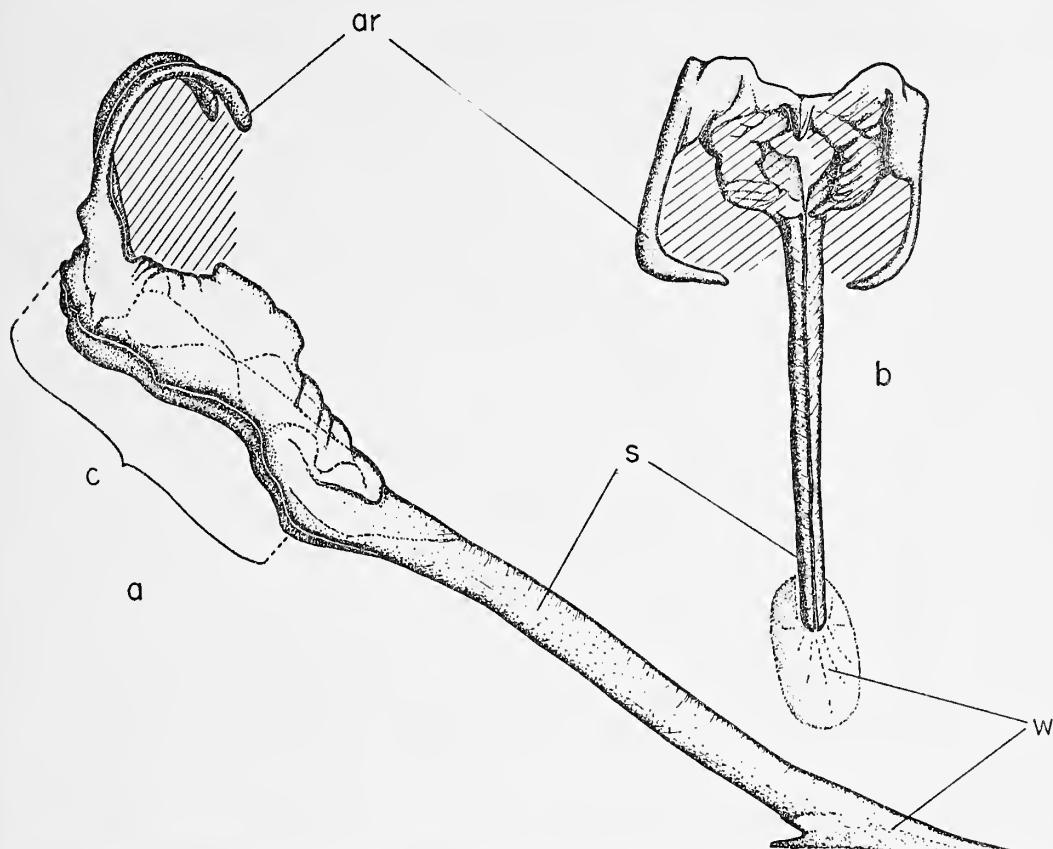
TEXT-FIG. 4. Spermatophore of *A. barbadensis*. **a**—Lateral view; the right-hand side is that from which the female approaches to take up the sperm. **b**—Dorsal, slightly lateral, view showing the face approached by the female. The position of the two sperm masses is indicated by the cross-hatched areas just above the capsule portion of the spermatophore, **c**, where they are normally held by the arms, **ar**, of this region. Stem of spermatophore, **s**; flat basal portion which is cemented down onto the substratum, **w**.

ward and crouches on top of the spermatophore, moving his body slightly as if orienting himself correctly in respect to it. Once settled, the male normally remains motionless for up to five minutes. Apparently it is during this time that he places two masses of sperm in position on the proximal end of the spermatophore. Certainly up to this point the spermatophore has been empty of sperm.

The male slowly rises from the spermatophore and steps back a few centimeters. He quivers and the female which has so far remained immobile comes forward, her feelers guiding her towards the spermatophore (Text-fig. 4). Finally she crouches over it, applying her genital region to its proximal end. She jerks forward against it, usually several times in quick succession though sometimes there is a thirty-second interval between the first and second attempt.

She then stands up with the two masses of sperm caught partly beneath her genital oper-culum. The male becomes active once more and taps the female rapidly for about fifteen seconds. When she moves away from the empty spermatophore, the male eats it. The two animals then separate and there is no evidence of aggression.

Finally, in this section on the reproduction of the Phrynichida, it may be mentioned that electrical stimulation of the genital area of a living male *D. variegatus* can cause the production and extrusion of a spermatophore. When low intensity shocks are first applied, the operculum will be lifted slightly and the genital cones be extruded. Presently, from between and posterior to these, a larger organ begins to appear. This is a many-lobed structure which will be referred to here as the "genital body" (Text-fig. 5). Further gentle stimulation causes the secretion of an amount of transparent, very sticky material, presumably that which normally cements the spermatophore to the substratum. Then, also from between the lobes of the genital body, the
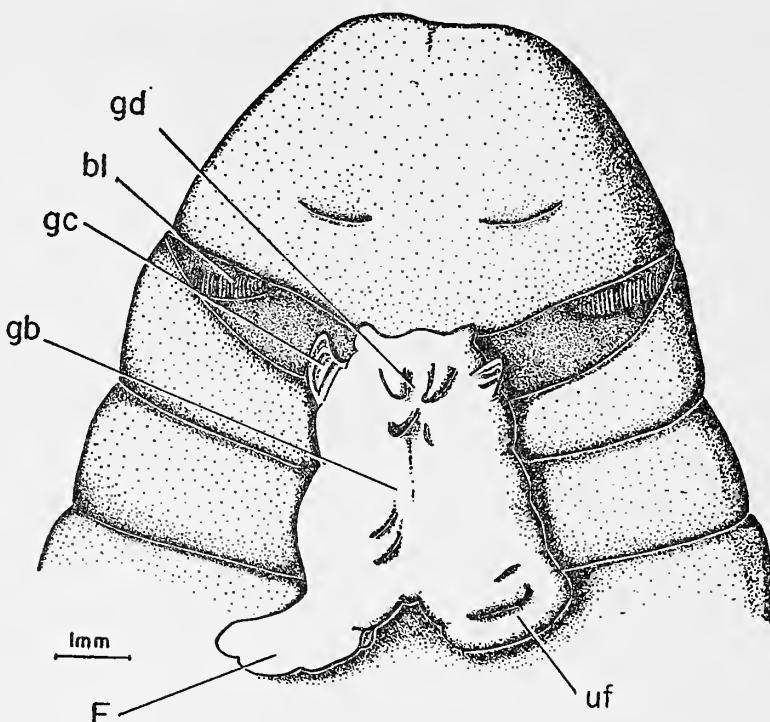
TEXT-FIG. 5. The genital region of a male *D. variegatus* showing the "genital body", **gb,** which has been extruded from the genital opening after electrical stimulation. The lobes of the genital body are somewhat asymmetrical in this example, so that the flap, **f,** of the right side is still tucked in on the left, **uf.** The genital cones have been displaced laterally and anteriorly and are only just recognizable, **gc,** in the drawing. The spermatophore is extruded at the point marked, **gd,** in the mid-line and between the various lobes. The striations, **bl,** represent part of the first pair of book-lungs which are visible under the genital operculum.

actual spermatophore itself is extruded. In such artificial conditions the production is never successful and the structure could clearly not be used for transference of sperm by the animal concerned. The use of such stimulatory techniques was reported by Piza (1950) working on a scorpion, *Tityus bahiensis*. Here a structure, which subsequent work has identified as the spermatophore, was partly extruded from the animal. In the case of a South African scorpion subjected to similar treatment, not only was the skeleton of the spermatophore ejected, but also a large part of the glandular apparatus which secretes it. Thus it should be borne in mind that the eversion of the "genital body" in *D. variegatus* may well be an artifact due to the abnormal stimulation and that in natural production of a spermatophore this does not occur.

DEVELOPMENT

It is known that in the Phrynichida, Schizo-

mida and Thelyphonida, the eggs are attached beneath the abdomen of the female after they are laid, a phenomenon that occurs also in the pseudoscorpions. The eggs of *A. barbadensis* and *D. variegatus* are held together in a fairly tough egg-case consisting partly at least of chitin. According to Millot (1949) and Lawrence (1953) the cavity within the egg-case is continuous with that of the female genital organs until the young are freed. In the case of *A. barbadensis* this is not so; the anterior end of the egg-case is a tough dried stalk which is held in position just beneath the genital operculum by the pair of sclerites mentioned earlier (p. 29 and Text-fig. 3c). This coupling of the anterior end may occasionally come loose and the animal is apparently incapable of hooking it up again. When this happens, the case is merely left attached by sticky threads to the abdomen. Occasionally, however, the whole attachment fails and the egg-case is dropped to the ground. In

one such instance, the female then ate the young and their case.

As Lawrence and Millot have observed, the abdomen of *D. variegatus* may be considerably hollowed out so that the egg-case does not project much below the normal level of the abdomen. The lateral margins tend, in fact, to overlap the edges of the egg-case and thus insure better protection. In *A. barbadensis* this hollowing of the abdomen is far less marked and the egg-case tends to hang down below the normal level of the abdomen, especially just before hatching.

The egg-case is secreted when the eggs are laid. It appears as a semi-transparent, colorless material which toughens and darkens during the subsequent twenty-four hours. It consists of two layers, an outer one which encloses the whole and a thinner inner layer which is continuous with packing material which lies between the eggs and the stalk attaching the case to the female.

It is not known how long the eggs remain within the case but they can certainly be carried for as long as a month before hatching. Emergence from the egg-case takes place during the night or early morning as a rule. The young come out through a ragged slit at the posterior end of the case. About twenty-four hours before the hatching this part of the egg-case can in fact be seen to have become softened and partly freed from the abdomen. Emergence may take as long as the whole night, the young easing slowly out of their own first exuvia as well as the partially liquified case. As they become free, they climb back onto the female. The remnants of the egg-case, the egg-shells and exuvia remain attached to the female until the young desert her several days later.

The young scorpion-spiders, *A. barbadensis* numbering from 15-30, *D. variegatus* up to 50, cling onto the abdomen of the female, covering both the ventral and dorsal surfaces, a phenomenon which occurs also among thelyphonids, as shown by the illustrations given by Strubell (1926) and Yoshikura (1958). They have never been seen on the prosoma and if one is dropped there experimentally, it will immediately climb back to the abdomen. It is not clear why this is so, either in terms of what controls the behavior of the young or what selective advantage is given by such a distribution of the young on the parent. Among scorpions, the female does not appear to be incommoded by the young which cling onto her prosoma any more than by those on the abdomen.

Newly hatched *A. barbadensis* are very soft and dusky pink; in *D. variegatus* the abdomen is light green. The abdomen is relatively much longer at this stage than it is in the adult and eleven segments are far more easily recognized. The feelers are folded up and, like the pedipalps, they are not used during this instar. The legs, however, attach the young very effectively to the female and one of the young animals can be disengaged only with great difficulty. If indeed a few are detached and strewn around the female, they make but feeble attempts to climb up again and only occasionally succeed. The female does not help in this at all, and in fact she merely shakes them off her legs if she can. She may touch one tentatively with her feeler for several seconds, then suddenly lunge forward, catch it on the spines of the pedipalps and immediately begin to eat it. Observations in which one or more of the young were eaten were made on four females and there is no evidence that they would not have eaten the entire broods if given the chance. In two cases the young had been hatched outside the laboratory so that there is little possibility that the behavior was abnormal. This leads to the conclusion that there is no maternal behavior towards young scorpion-spiders that leave their perches on the back of their mother.

This is in marked contrast to the complex maternal patterns shown by many other arachnids, such as some of the spiders and scorpions. In terms of selective advantage, the explanation for this does not seem to lie in the young scorpion-spiders being more firmly fixed to the parent than are young scorpions; both appear equally well attached. It seems possible, however, that the two different types of response can be correlated with the reactions of the mothers to a threatening danger or a disturbance. In such circumstances, a scorpion will stand and threaten with claws or sting, otherwise it remains immobile. In only a few cases will it run away, and if flight occurs, it is usually brief.[5]

A scorpion-spider, on the other hand, stands and tries to defend itself only if it has already been partly damaged. Very occasionally it will remain still and perhaps be overlooked; almost always, however, it starts to run immediately. The flight is broken up into short dashes sideways but as a rule the animal finally comes to rest several yards from the site of the original

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[5] Possible exceptions to this generalization are such flattened, rock-dwelling scorpions as the South African genus *Hadogenes*, which may display an escape response. This, however, is not shown by females carrying their young, so that at such a time their behavior is similar to that of the other scorpions mentioned above and not to be compared with that of the phrynichids.

disturbance. The point is that, if young scorpion-spiders are knocked off their mother, they usually have no chance to climb back because their mother will normally be some distance away by the time they are ready to do so. It is of no advantage for the female to have developed behavior which would allow her to distinguish her own young from any other helpless, wiggling arthropod which might be food on the ground. In the case of the scorpion, mother and young are still together after an "attack" has passed and it would be advantageous for a female to possess a behavior pattern that actually helps the young to remount, and even more so for her to recognize that they should not be eaten. A further consideration which may prove important in such an explanation of why the phrynichid female has evolved no recognition of her young is that these animals, unlike scorpions, possess no "homes" in which they live and to which they return. It would thus be of interest to know of the Thelyphonida and the Schizomida—more especially as females from both these orders are reported to live in burrows, at least when they have eggs (see Gravely, 1915; Millot, 1949; and Yoshikura, 1958).

On their mother's back, the young phrynichids make almost no movement during the second intermolt period. This lasts four to six days in *A. barbadensis*, up to 12 days in *D. variegatus*. The second molt appears always to begin during the morning. The length of time taken for any one individual molt varies considerably, from six minutes to almost three hours. There seems to be a preferred site for this event—the posterior part of the abdomen of the female—and most of the young do not begin to shed their skins until they can move towards this position. The molt begins with a number of cheliceral movements. Then a blister-like swelling arises on the carapace. This pulsates slightly and a split gradually appears round its anterior margin. The animal bulges out of this slit. Of the limbs the first to be freed are the chelicerae, then the pedipalps and lastly the legs. As the old cuticle is sloughed back, fluid within the body of the young can be seen to be pulsating rhythmically. When the new cuticle is uncovered, it is almost colorless but rapidly becomes greenish-blue and darkens over the next couple of days to a brilliant metallic green. The old skins are not eaten by mother or young and they fall from the mother's back as pieces of pink fluff. Like the first exuviae of scorpions and unlike their own late stages, the skins that are left after this molt are very thin, soft and flexible. This is presumably a reflection of the fact that the animals are markedly unsclerotized during their early instars.

Unlike many scorpions which remain for some time on the female after they molt, the young scorpion-spiders climb off within a few minutes of freeing themselves of their cast skins. This climbing down is no accident and is quite "deliberately" done, for a young third instar nymph will immediately run off its mother if replaced.

There is a marked change in the behavior of the phrynichids after their second molt. Once they reach the ground, they run around quickly, feelers are unfurled and they tap tentatively at objects near them. There is a noticeable avoidance of light. None of this behavior was of course present when the young were on their mother. Within two days they are capable of catching and eating termites provided for them, and are clearly independent of the female and, indeed, can be found at this stage running about by themselves in the field.

PHYLOGENETIC DISCUSSION

It has already been said that the study of the behavior of the Pedipalpi might throw light upon the phylogenetic relations of the different groups which have been lumped in this order. Many of the observations here recorded merely serve to emphasise the need for comparable studies on the other two members of the Pedipalpi, the Thelyphonida and the Schizomida. Of the biology that has been described, however, three aspects appear as though they might provide material of significance in relation to the phylogeny of these groups, namely, feeding, sexual behavior and the general reactions of defence and offence. The importance of feeding has already been implied in the stress which Petrunkevitch lays on the feeding organs in his classificatory system. It is, however, abundantly clear that more work is still needed on the mechanism of feeding in the Phrynichida, while even less is known of the details in thelyphonids and schizomids (Snodgrass, 1948). It is perhaps significant that although the filter-plate apparatus in the Phrynichida is superficially like that of scorpions, there are no associated limb movements in the former.

Courtship likewise can be but sketchily compared in the three groupings because actual mating has not yet been seen in the thelyphonids. From descriptions of the preliminary behavior (Fischer, 1911; Gravely, 1915) it seems that the male in this order grasps the female first with his pedipalps and subsequently with his chelicerae, during which the two animals face each other. Schizomids also promenade before mating takes place (Sturm, 1958) and a cheli-

ceral grasp occurs, but here, however, the grasp is quite different from that reported for thelyphonids. It is the female which holds the male and the part which is grasped is the specialized portion of his tail; consequently both animals face in the same direction. Hence it is possibly of little significance that the Phrynichida also differ widely, in having no mating grasp at all. Indeed such variations in detail of courtship may occur even among arachnids which are undoubtedly closely related; for instance among the pseudo scorpions a mating grasp may or may not be present.

Insemination is indirect by way of a spermatophore stuck down onto the substratum. Considered alone, however, the fact is of little significance as this would appear to be the primitive method among the Arachnida (Alexander & Ewer, 1957) if not among terrestrial arthropods generally (Angermann & Schaller, 1956; Gilarov, 1958). If the arachnids were originally aquatic forms in which fertilization was effected by "casual" meeting of sperm and eggs after both had been liberated into the sea, then the first step in the evolution of the spermatophore is perhaps exemplified by the behavior of water mites and some pseudoscorpions in which the male deposits spermatophores apparently haphazardly around him, with or without the presence of a female. With a drier and wider habitat there would be increased danger of desiccation of the sperm and perhaps decreasing chances of a female coming across such casually deposited spermatophores. Thus there would be selection for an association between male and female to be established before deposition of a spermatophore occurs and it is to be expected that such associations may have been independently evolved several times. Nevertheless the phrynichids and schizomids might be regarded as related insofar as the male has his posterior end towards the anterior end of the female while he deposits a spermatophore. Such behavior is in contrast to that of the pseudoscorpions, the mites and especially the scorpions where the spermatophore would not function if the female were forced to approach it from the opposite direction. However, the very specialized mating grasp of the schizomids makes it improbable that the position taken up during spermatophore extrusion bears any direct relationship to that of the phrynichids.

The marked dissociation of the acts of spermatophore deposition and sperm extrusion is unique and it is hard to see any advantage to the species from such behavior. It is, however, clear that the two events are completely independent. Thus on two occasions a male *Admetus* re-

turned, in one case three times, to a spermatophore when he apparently been unable to load it successfully at the first attempt. Another time a female *Admetus* walked away while the male was depositing sperm; the male chased after her, courted her once more to passivity and then returned to his dispositing of sperm. This dissociation possibly offers the advantage that should anything cause a faulty deposition of a spermatophore or disrupt the mating, sperm will not have been wasted. A somewhat similar situation occurs in *Tityus trivittatus* in which Bücherl (1956) has described a "reloading" of the spermatophore after the female had removed the first mass of sperm.

Petrunkevitch has postulated a close association between the Phrynichida and the Araneae, and the present observations can be read in support of such an opinion. It has been suggested (Alexander, 1962) that the sexual behavior of spiders may be derived from that of forms in which there was a dissociation of the act of loading a spermatophore from its deposition. This is the condition in the phrynichids. Further, it is easier to envisage the course of the evolution of spider mating were it derived from a pattern in which the members of a pair did not grasp and this again is a phrynichid character.

Finally we will consider what Manton (1958) would term "habits of life." It is this last type of behavior that is hardest to categorize distinctly, the facts are less definite, actions less stereotyped and more difficult to describe. As Manton says: "Habits of life which appear to have been of evolutionary significance vary greatly in their ease of recognition because they may not be exercised all the time." Nevertheless it is from this level of activity that an understanding of the general biology and the direction of morphological and behavioral evolution will emerge.

In considering the life habits of the groups of the Pedipalpi it is desirable to point out that the natural micro-ecological distribution of the animals is not markedly different. What is significant, however, is that the Schizomida and Thelyphonida remain within their burrows or in spaces in the soil while the Phrynichida run freely over it or hide in crevices—the animals may be referred to as being "of fixed abode" and "vagrant," respectively. Defensive behavior can be correlated with this difference. The "fixed abode" groups stay to defend themselves with cheliceral pedipalps or repugnatorial glands when concealment is no longer possible. The Thelyphonida are aggressive in captivity and large specimens may even damage human hands with their pedipalps. This is in complete contrast

to the emphasis among the phrynichids on camouflage or flight; the scorpion-spiders either sit still and are overlooked or get away quickly and unexpectedly with sudden and disconcerting sideways darts—behavior for which their flattened form, short abdomen and the sideways extension of their legs are well adapted.

The absence of attack as a defensive response in phrynichids is also partly reflected in an "inefficient" use of the pedipalps during prey-catching, for the scorpion-spiders frequently fail to hold prey at which they grasp. In natural conditions there must often be unsuccessful attempts or the prey must be weaker, smaller and consequently hunted more frequently. In either case accurate locating and careful stalking is important and for these two phrynichid characteristics are essential, the habit of roaming freely about and the possession of elongated feelers. Together with the latter must be considered the toilet behavior patterns involved in keeping them clean as well as the specialized pedipalpal brushes.

Though it is freely admitted that this is but the beginning of an understanding of phrynichid life habit, the number of anatomical and behavioral characteristics which can be correlated with this habit suggests that it has been of prime importance in controlling the direction of phrynichid evolution. When similar and more complete analyses are available for the Thelyphonida and Schizomida, it may prove possible to comprehend the true inter-relationships of these groups and their relationships with the other Arachnida.

SUMMARY

1. The general biology and behavior of two species of phrynichid, *Admetus barbadensis* Pocock and *Damon variegatus* Perty, have been studied. A description is given of their habitat. food and manner of feeding, their drinking and their cleaning patterns.

2. Behavior which does not lead up to courtship but occurs between two members of the same species is described; much of this behavior consists of threatening contests in which the delicate feelers are used as "weapons."

3. The main course of courtship is described. Insemination is achieved by means of a spermatophore which the male deposits on the substratum and from which the female picks up the sperm mass. This method of mating is compared and contrasted with those occurring in the schizomids, scorpions, pseudoscorpions and some of the mites.

4. Events associated with the electrical stimulation of the genital area of a male *D. variegatus*

are described and discussed in relation to the production of a spermatophore.

5. The manner in which the eggs are cared for after they have been laid and the hatching of the young is described, as well as general observations on their behavior in contrast to that of the adult animals. An hypothesis is put forward attempting to explain, in terms of selective advantages, the absence of any maternal reaction from the female phrynichid to one of her young struggling on the ground in front of her.

6. The behavior recorded here is discussed in relation to its bearing on conclusions about the inter-relationships of the Phrynichida, Schizomida and Thelyphonida.

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6

Breeding Activities, Especially Nest Building, of the Yellowtail (*Ostinops decumanus*) in Trinidad, West Indies[1,2]

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(Text-figures 1-4)

MOST AUTHORS AGREE that two families excel at building complex nests—the Icteridae of the New World and the Ploceidae (True Weavers) of the Old World. This paper reports nest building and some associated breeding activities of the Yellowtail, *Ostinops decumanus,* of the Icteridae, as observed during ten days in late January, 1960, at the New York Zoological Society's Department of Tropical Research field station at Simla, Arima Valley, Trinidad, W. I., and discusses relevant literature.

Since F. M. Chapman (1928) made a three-year study of the courtship and breeding activities of Wagler's Oropendola, *Zarhynchus wagleri,* on Barro Colorado Island, Panama Canal Zone, the most comprehensive reports on the flamboyant displays and the complex hanging nests of this group of the Icteridae are by Skutch (1954) on the Montezuma Oropendola, *Gymnostinops montezuma,* and the Yellow-rumped Cacique, *Cacicus cela;* by Tashian (1957) who studied the Yellowtail at Simla; and by Schäfer (1957) who studied *Ostinops decumanus* and *Psarocolius angustifrons* in detail. Although these papers do not include critical analyses of nest-building motions, they allow me to make comparisons of the nest-building techniques. (These papers are referred to below without citation).

The four species of oropendola—*angustifrons, decumanus, montezuma* and *wagleri*—appear to be very closely related, and as a systematist trained in a field other than ornithology, I would not hesitate to include them in the same genus. However, the currently accepted generic names are used here. Table 1 lists outstanding features of the behavior during courtship and nest building shared by members of this group. Nest building suggests that they are close to the caciques—just how close may be revealed in further studies.

HABITAT

The Yellowtail nests in large numbers in the erythrina trees, *Erythrina micropteryx,* also called "bois immortel," introduced into the Arima Valley to provide shade in the cocoa and coffee plantations (Text-fig. 1). Although the cocoa, *Theobroma cacao,* coffee, *Coffea arabica,* and banana, *Musa paradisica,* trees planted under the erythrina are also introduced, all are readily accepted by the native birds. The undergrowth of most of Trinidad is cleared several times a year with long knives, locally called cutlasses. The cutting suppresses the heavy secondary growth that would compete with the local crops. Rising above the understory to an average height of 50 to 150 feet are the erythrina, whose orange-red blossoms cover their crowns early in the year at the close of the rainy season. Schäfer describes identical habitat for Yellowtails in Venezuela.

The ends of the erythrina branches are ideally suited for the attachment of the Yellowtail's nest, because (Text-figs. 3, 4) of the whorls of stiff, dead leaf- or flower-bases that extend two to five inches along the branch at the bases of the smaller branches. The bases of the nests we saw were woven into these burr-like structures. Furthermore, the trees are tall, with smooth bark, and at the top they spread umbrella-like

TEXT-FIG. 1. Part of Yellowtail nest colony in *Erythrina* tree. Nests 1 and 18 were studied during site establishment; nests 9, 10, 18 and 19 were studied during building of the sleeve, closing the entrance, and weaving the bag; nests 13, 15 and 19 were studied during weaving the bag and closing the bottom.

crowns which do not interfinger with each other. As Skutch points out, these characteristics provide sites that protect the nests from predators (chiefly lizards and snakes). He describes the destruction of a colony of Yellow-rumped Caciques to which a snake found access by vines growing up the trunk. Schäfer comments on the form of branch-tip preferred for nest establish-

ment and the umbrella shape of trees chosen by *decumanus,* comparing them with the requirements of the forest-opening species, *angustifrons,* which places its nest on the wall of vegetation along roadsides.

TERRITORIAL BEHAVIOR OF THE MALES

Erythrina trees are scattered 40 to 50 yards
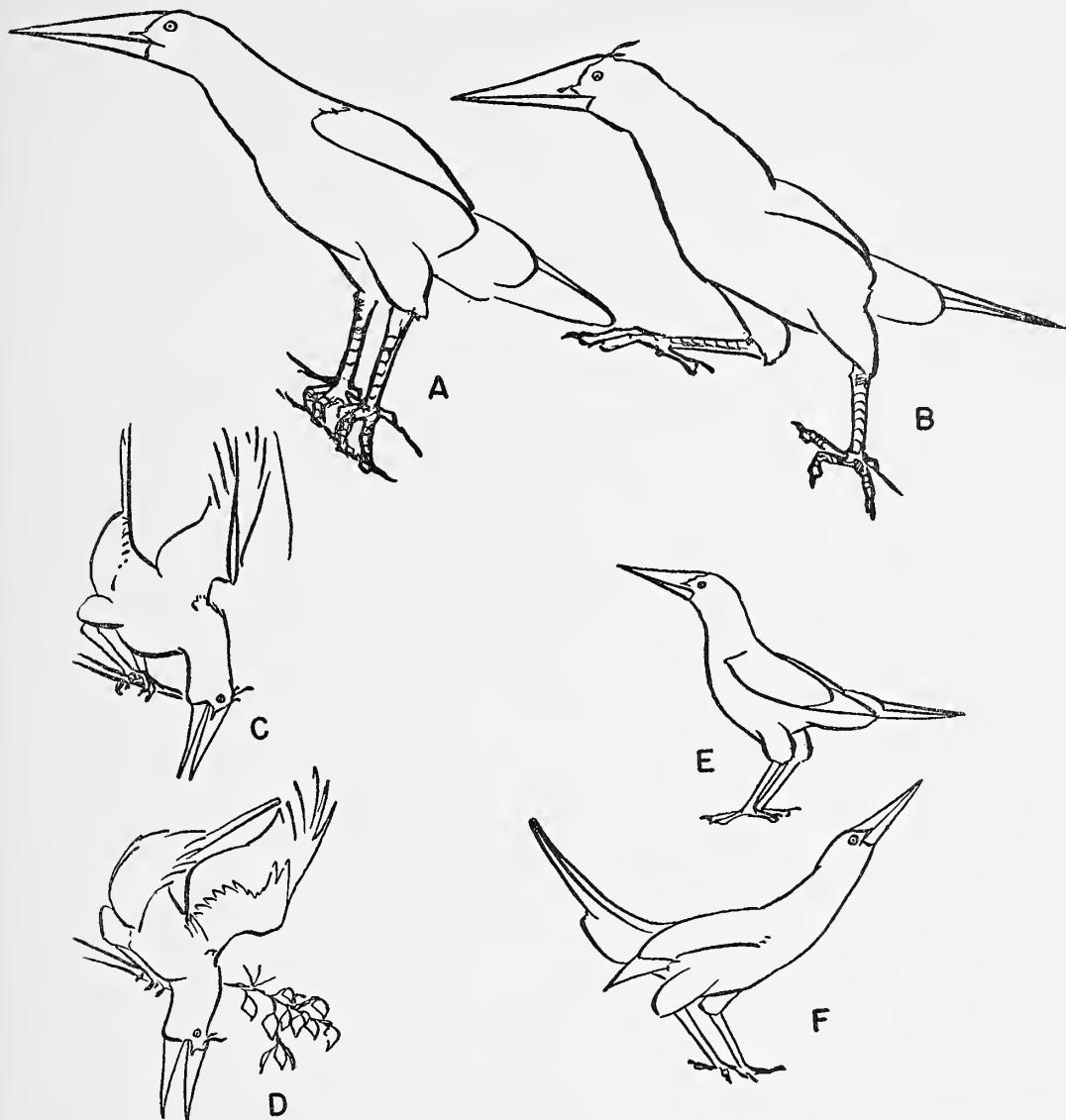
TEXT-FIG. 2. Display postures of Yellowtails. **A.** Anxious, subordinate male. **B.** Dominant male approaching intruder. **C.** Low level song posture given when alone, primarily territorial. **D.** High level song posture given when near a female, primarily sexual. **E.** Anxious and aggressive female in squabble near her nest. **F.** Soliciting female.

apart on the steep hillsides of the Arima Valley. Each dominant male Yellowtail appeared to occupy a territory covering two or three adjacent trees. The males in the colonies which Chapman and Skutch studied did not seem to have a territory or a set relation to any particular group of females. I agree with them that as soon as one male made a supplanting attack on another, the attacked bird left, suggesting dominance and territory defense, but I saw no territorial fights, nor did Schäfer. Schäfer's detailed discussion of territory in *decumanus* and *angustifrons* shows site tenacity and hierarchical arrangement among dominant and subordinate males around a colony tree. There are differences of degree, but in both species subordinate males intrude almost undisturbed, especially at the period of copulation.

When an "intruding" male came into a tree (even the nesting tree itself), he often spent as much as ten minutes there without being attacked. If the resident male did pay attention to

the newcomer, however, he moved into the tree or branch, flying directly at the intruder or perching 20 yards away, then walking or hopping toward him with neck swollen and head point up slightly (Text-fig. 2B). Soon the intruder (Text-fig. 2A) left and shortly afterward both males sang. If, however, an intruding male bowed and sang, he was often rushed by the territory owner. In one instance the intruder left soon after the owner bowed and called twice.

The male has half a dozen song or patrol perches at which he spends most of his time. When active, he spends four to ten minutes at each perch. When inactive, he may be difficult to find—either he is away from his tree or sitting quietly on one perch. Schäfer has notes on the schedule of activities of territorial males and females.

I heard some sing all day, and the most active singing between 0600 and 0900, and between 1600 and 1930, local time, as did Schäfer. Tashian recorded the frequency of singing and reported no peaks, but that may have been because his study was made earlier in the reproductive season.

Song and Display.—The song is described in detail by Tashian, who used moving picture film to analyze and time the postures which accompany it. Schäfer separates territorial from nuptial song. As a bird starts his nuptial song, he drops his head steeply between his feet and raises his tail over his back, stiffly fanning his under tail coverts which, like his tail, are yellow. The bird then usually gives two hollow, gurgling calls and, standing in a deep bow with the feathers of his neck stiffly raised, gives a rattling trill (*eeeeoooo-eeeeoooo*, or *eedy-eedy-ooo*), which grades into a continued rustling made by flapping his relaxed but raised wings (Text-fig. 2D); then he stands up. He may repeat this call as often as every twenty seconds for two hours, but usually the call is relatively infrequent, given about once every three or four minutes. Schäfer reports every three minutes, or 10-20 times an hour, averaging 100 times a day. I found this call most frequently directed toward a single female or group of females. Schäfer found the noisy flight between perches so regular a prelude to this song as to be a part of it. He found that this call was less frequently given than the territorial song, and I agree.

The territorial call starts with (1) a rattling gurgle, or (2) a hoarse *tsteeee* or *tsreee-kleee,* ending in a series of "plop"-like calls—*ka-wow-wow-wow.* I did not see the posture which accompanied it and heard no wing-rustling with it. Usually it is given by an isolated male and, I believe, not necessarily in the presence of females. Schäfer says that the cry is given with raised and weakly beating wings, and with plumage not fully displayed (Text-fig. 2C).

The singing bird, especially away from a nesting tree, may alternate his song with feeding in the blossoms of the erythrina tree, but usually when he is singing he spends the time between songs moving among his trees, standing, peering around in the tree, preening wings, flanks and neck, ruffling feathers, scratching, pecking at his feet(between the toes) or wiping his bill. When in a nesting tree, the male occasionally flies vigorously (his wings make a deep resonant sound) to perch on the side of a nest that is completed or is being built. He lands with head already down and neck swollen, and gives his full song, perches stiffly, with crest raised, neck swollen and blue eye glaring, for ten or fifteen seconds, and then flies, usually to perch on the branch at the base of this same nest. I saw a male fly at and replace a female who had just flown in and landed on the nest, and several times a male responded to the arrival of a female or a group of females with a bow and a song. The male was especially likely to respond with song to the arrival of females if he had recently driven away another male.

Most of the time, even when the male flies to her nest, the female pays no overt heed to his activity. Occasionally she is evidently interested and watches him, usually with her head up and feathers sleeked (head-up "threat" of icterids, with some "fleeing tendency," Text-fig. 2E). I found no direct relation between song display and copulation. Schäfer does not suggest any close relation and points out that during the copulation period territoriality seems to be minimal.

During the day, males are usually isolated on territories, although many (young and inferior males, Schäfer suggests) visit other males' territories or nesting trees. In the evening males stay isolated in the crowns of the erythrina trees until after the evening roosting flights of females, which take place between about 1800 and 1830. Then males leave their territories and fly singly to the communal roosts which, in the Arima Valley, are in a large clump of bamboo at the bottom of the valley below Simla. On their roosting flights, females in groups of three to thirty come from several miles, usually in short flights between crowns of erythrinas. They stop in the territories of actively singing males and often engage in precopulatory actions. Males are the last to settle in the bamboo roosts. They start to sing on their trees again before the sun is up.

The females of any one nesting tree readily visit territories of other males, and I saw copula-

tion less often in nesting trees than in other trees where a male was on station but where there were no nests.

TERRITORIAL BEHAVIOR OF THE FEMALES

I counted 1, 3, 5, 22 and 43 nests in five different trees, each in a singing male's territory (Text-fig. 1). Females usually in groups of a dozen, but at times several dozen, fed in the cocoa and citrus trees and moved along the ridges down into the groves to gather nesting material and food. Actively building females spent much of the day working at their nests, while groups of females not especially attached to the nesting tree visited it for several periods of twenty minutes to half an hour.

As Skutch and Chapman report for their oropendolas, a number of Yellowtail females operated as a group and placed their nests on the same branch or on a series of branches close together. These nests were consistently placed on the leeward side of the tree and on the outer and upper part of the crown, at least 40 feet above the ground. Schäfer agrees, and has many details on choice of colony trees, location of nests, calendar and schedule of events which led up to colony establishment. He stresses the importance of weather changes which start the cycle, but does not mention subgroups of females within a colony.

When close together in what appears to be a squabble over the nest site, the females stand with heads raised to a 45° angle and with tail partly raised (Text-fig. 2F). I saw no fighting such as recorded by Skutch and Chapman, but frequently heard a nasal hiss, *garreeoo* or *aaah*, from birds in this circumstance. It resembled part of the song of a Starling, *Sturnus vulgaris*. The females crowded their nests together even within the limits of the group and four of the nests I watched being built were woven into a neighbor's or a previous year's nest. Schäfer mentions hostility of females to males and their fierce attacks on inept immature males that trespass at their nests.

PROGRESS OF THE BREEDING CYCLE

Chapman, Skutch, Beebe (in Tashian) and Tashian agree that nest building starts at the very end of December and in early January. This coincides with the end of the rainy season. Chapman believed that for Wagler's Oropendola the start of the nesting season is more accurately associated with date than with the last of the rains, but Schäfer shows in detail how the downpours that come with cold, northerly winds start the cycle in *decumanus* and how humidity controls the start in *angustifrons*. Chapman reported

the beginning of the breeding cycle as being signalled first by the arrival of individual males in the colony tree. Both Chapman and Skutch say that the real start is the arrival of groups of females to inspect the branches of the colony tree. Schäfer shows clearly that in *angustifrons* the males' territorial activity is a critical stimulus for the start of the nesting activity by females. If he stops his display, they stop.

Copulation.—The male Yellowtail sings in his tree, occasionally flies noisily and perches with a group of females who are preening or moving among the branches. The females may ignore him or may move away nervously, with their heads slightly raised and feathers sleeked (Text-fig. 2E). This activity continues through the early stages of nest building. Schäfer shows that copulation receptivity appears in females of both *decumanus* and *angustifrons* as they finish the nest bag and line it.

When receptive, the female flies to a branch near a male. Twice I saw a female fly to a male from inside her nest, and on other occasions females came "out of the blue" into an isolated song tree. The female perches above or near the male with feathers sleeked, head raised and tail raised or horizontal, and may almost imperceptibly flutter her wings. The male, with neck swollen, hops and walks along the branches to perch below and beside her. The female squats and flutters her wings, with head and tail slightly raised; the male mounts for about ten seconds while both birds flutter their wings. The male dismounts and, in my observations, flies rapidly away at once. On landing, he wipes his bill and continues his patrolling and singing. After ruffling and shaking her feathers, the female usually either started to preen or flew off. Schäfer's notes are very brief but agree with these. Tashian reports that the male sang and displayed and pecked at the female's cloaca before copulation, and that he displayed again after copulation. I have notes on several sequences in which a male approached a female as in copulation and then pecked violently at her cloaca, but these preliminaries did not lead to copulation and suggest rejection by the female.

Asynchronous Activities of Groups of Females. —All authors agree that many females start nests much later in the season than the main group. Chapman felt that some may have been second nests. Schäfer emphasizes the place of immaturity. In one of Chapman's groups of late-nesting females, building was interrupted and then the beginning of the rainy season caused them to abandon the colony site. Skutch found a colony in northern Honduras feeding nestlings in Sep-

tember. As with so many birds, the breeding cycle of the oropendolas must be started by a regular annual time-giver, and breeding continue until interrupted by some internal or environmental time-giver—in this case, the next rainy season.

There is also variation in the timing of an individual female's breeding during the species peak in late January. At the tree I watched, there were about a dozen females prospecting, four nests being started, six nests being built, about thirty idle nests or with females incubating, and at least five nests with females feeding young. Females regularly came and perched near the idle nests and clucked, or they flew in and perched head down in the entrance for twenty seconds, turned and perched looking out for thirty seconds to a minute, then flew off.

NEST BUILDING

Building Material.—(See Table 1 for details of nest-building materials used by the five species. Schäfer describes them in detail for *angustifrons* and *decumanus*).

Schäfer says that *decumanus* collects materials among the trees and off the ground, at a distance from the colony, while *angustifrons* collects material low in undergrowth or on the ground under the colony. Skutch describes the collecting of fibers underneath a banana frond by a female *montezuma,* and the actions are similar to those used by (1) the Baya, *Ploceus philippinus,* in India when nipping and tearing strips from the base toward the tip of a rice leaf, *Oriza sativa,* (Ali, 1931); and (2) by the Village Weaver, *Textor cucullatus,* tearing leaves of Elephant Grass, *Pennisetum purpureum,* (Collias, 1959).

My observations showed that *decumanus* uses chiefly long, fibrous strips and grass. The materials are green when brought to the nest, but turn brown in a day or two. In many cases the fruiting heads of the grass (resembling *Panicum*) were still visible. On other occasions small vines with tiny green leaves (resembling the *Solanum* family) were used. Schäfer says that the supports and weave are chiefly (80%) liana tips, and that the packing between is entirely Spanish moss, *Tillandsia usneoides* if available. He describes the material used by *decumanus* as slender and fine, in contrast to the characteristically coarse and turgid material available in the forest interior and used by *angustifrons.*

Skutch describes *montezuma* folding over the strips from the banana frond in order to carry long pieces. Yellowtails brought their material in unfolded or gathered into loops in the bill,

and often the material streamed far out behind the bird as she flew (Text-fig. 1).

When the female Yellowtail starts to build, she uses pieces that average 30 to 45 cm. long; then, as she finishes the base and builds the supports at the entrance, she brings fewer pieces per trip and they are 60 to 100 cm. long. She brings many shorter pieces again as she weaves the sides. When weaving the bottom, she brings a few long pieces (100 to 150 cm.). These appear to be strips of banana leaf.

Skutch speaks of violent squabbles over nest-building materials in *montezuma* and no squabbles in the Yellow-rumped Cacique. Schäfer describes frequent violent fights in *angustifrons* and few in *decumanus*. Chapman describes the stealing of loose ends from slovenly nests or from those of absent birds by *wagleri,* as does Skutch in *montezuma.* These two species may demolish a messy nest. Schäfer comments that stealing is usual in *angustifrons,* infrequent in *decumanus.* I saw very little grabbing of material from other nests. On one occasion a female repeatedly flew past a nest with a moplike mass hanging below the finished entrance, and each time she grabbed a hanging, loose end and tried to fly off with it, usually unsuccessfully. On another occasion, a female perched several minutes on the outside of a nearly completed nest, pecked and seemed to try to pull out the tiny, still-green fibers sticking out or looped through the brown weave. Another time a female perched on the outside of the nest and repeatedly pushed her bill through the weave, opening it and making a series of fairly large holes, but not pulling anything out. In each case the visitor left when the builder came back, but in no case did the builder chase her. Schäfer says that young males make holes in the sides of nests during the period when females are receptive.

Schäfer discusses nest building in *decumanus* and *angustifrons,* emphasizing differences in location, placing of the nest, and the materials used. His data are very largely on *angustifrons,* and although he describes the phases of building (anchoring the nest and weaving; building the apron; building the ring and the future entrance; building the bag; and bringing the nest lining), he does not treat in detail the movements involved.

Phase 1: Site Establishment.—When the female is establishing her nest site, she spends from five to fifteen minutes perched at a fork in a branch at the tips of the long branches of the erythrina (Text-fig. 3A and B). She walks and hops, alternating her feet, along the main part—peering, looking under and over the forks

near the tip. She spends much time peering out across the valley. Skutch and Chapman describe frequent squabbles in groups of females inspecting branches. Schäfer describes threat postures, but no real fights. I found the females inspecting alone, and saw no squabbles among the few birds prospecting. There were several squabbles among the females on lower branches where nests were already established.

When the female first brought material (long grass or vines), she perched and looked around, moved, looked around, flew to another branch, stepped on the grass and gathered another loop, then flew to another part of the tree. At two sites, where females had been prospecting on previous days, I watched a female bring long grass in her bill and, perching on the branch, look, move, look, then push it into the dead leaf petiole bases at the joint (Text-fig. 4D). These females brought several loads before the grass remained in place. The female may or may not step on the grass with one foot (Text-fig. 3C); she may grasp an end in her bill, gather another loop, pick up all the material, and fly off again; she may do no more, and just fly off; or she may take bits of the grass and push them down into the clump of dead leaf bases, then reach around the branch and pull a strand up around the branch (Text-figs. 3E & 4A); or she may pull a loose end around a leaf base and poke it into the mass of material with a short shake (four or five times) of her bill—the tremble-shove (Lorenz, 1955). When building the base of the nest, the female pulls ends *around* and uses the bill-shake more conspicuously than when weaving the sides of the nest.

I found the females hesitant and irregular in their activity when establishing the nest site, but I think this may have been caused by my presence. Schäfer suggests that activity during this period is readily interrupted.

Phase 2: Establishment of the Nest Base.—The female brings grass and may put her foot on the newly-brought material (Text-fig. 3C), or may merely push it into the tangle already in the leaf base. Soon after some material hangs down, she pushes the new material into the mop (apron, *tablier*) just under the branch. When the mop is short, she usually pulls only a little and just "fiddles" with loose ends, then flies off. As the mop lengthens, she tucks the new material under the branch and, reaching over to the other side, grasps a piece of grass in the very tip of her bill (Text-fig. 3D), often with a little shake as she takes it. She pulls this gently or firmly toward her and tucks it into the grass on her side of the branch, with two or three pokes and four or five shakes of her bill. Or she takes a piece

of grass from the side nearest her, pulls it over and tucks it into the grass around and behind the branch, with the same bill-shakes. Usually she worked two, three or four times from her side of the branch, then shifted to reach behind and work from there. She often worked for several minutes without touching the green grass which she had just brought. I did not establish that she worked with the same piece of grass, but the fact that she did no alternate pecking on one side and tucking into the other with the reverse, suggests that she was not working with a particular blade.

The only action I saw during the building of the base was "peck-pull around-tuck"—with the grass held in the leaf base or under the female's feet. She put her foot on the nesting material only during the first day or two (as Schäfer also reports), but worked on the base for twice that length of time. As more grass was added, the female pulled harder at the loose and long ends of the grass.

Comment.—My notes show consistent differences in the construction of the nest base by the Yellowtail, when compared to the other oropendolas and cacique. According to Chapman and Skutch, *wagleri* and *montezuma* weave the pliant material around and around the branch, and they suggest that the bird wraps an individual piece and ties it to the branch before working with a new piece. Schäfer's notes agree more closely with mine, but in *angustifrons* he suggests that when the female brings in the first long fibers, she does give each one individual attention in wrapping them around the branch, and further, that she may perch and swing on the hanging end as if testing its security.

Phase 3: Transition to the Sides of the Nest.—Soon there is a loose mop of fibers about 10 cm. long hanging from the fork of the branch and extending 7 to 10 cm. along both sides of the fork, and then the female shifts to the next phase of building. Now, instead of perching with both feet on the branch (Text-figs. 3C, D, E & 4A), she perches with one foot on the branch and the other on the mop which is hanging from the branch (Text-fig. 4B). Her weight on the hanging fibers causes the apron to elongate. The female still pokes the grass into the woven material near the branch, but now pokes it only into the mop and not on top of the branch. She still consistently pulls the grass around something (either the branch or the edge of the material hanging from the base) and uses the peck-pull around-tuck movement. Thus she weaves over the branch and also binds or "overcasts" the edge of the material on the two "open" sides of the nest's horseshoe-shaped base (Text-fig. 3F).

TABLE 1. COMPARISONS OF BEHAVIOR IN COURTSHIP AND NEST BUILDING

| Character	*Gymnostinops montezuma*	*Zarhynchus wagleri*	*Ostinops decumanus*	*Psarocolius angustifrons*	*Cacicus cela*
Roosts	Bamboo		Bamboo	Palms	
Male's call		chuck	chac	quic	
Alarm	cack	chack-chack	kak-kak-kak	chak-chak	
Male's alarm panics colony	p	p	p	a	
Male's song	*tsu ta ta ooo tsreee kleee a wow wow wow*	Deep, liquid, "hope you choke," sputtering cackle, crash	Melodious *tschuudu du du du tshuuii wup wup wup*	Bell-like melody 3-6, soft thick crescendo to explosive 5-6	Brilliant and varied
Territory	Several males, 1 tree	Several males, 1 tree	Several males, several trees. 1 male dominant and subordinate males present	Several males, several trees. 1 male dominant and 2-3 subordinates.	Several males, 1 tree
Territorial song			*eedy eedy ooo cherie du du du wup wup wup*	Melodious and shorter than song, emphasis on 2 & 3	
Song bow	p	p	p	pa	
Raises on toes	p	p	p	pa	p
Neck swollen		p	p	pa	p
Eyes glare		Blue	Blue	Green-brown	
Tail up during song		p Flicked	p	½	p
Wing-waving during song	p	a	p	pa	p
Male flight noisy	p	p	p	pa	
Enlarged bill	p	p	p	p	p
Presence of crest	p Small	p	p	p small	
Courtship away from colony	p	p	p	a	p
Dark central tail feathers	p	p	p	p	
Females outnumber males	Several times	6 to 1	p	p	p
At least polygamous	p	p	p	p	p
Sex size-difference	p	p	p	p	p
Territorial fights	a	a	a	a	a
Female preens male's neck		p	a	p	
Male pecks female's cloaca			(a) p	a	p
Females associate in flocks	p	p	p	pa	p
Female threat	*raah* whine	*raaah* whine	*tcherie garreeoo* or *raah*	Hiss	
Female alone builds	p	p	p	p	p
One tree	p	p	p	a	
Nest at end of rain	p	p	p	a	p
Short-distance migrant	a	p	p	a	
Female territory		p	p	p	
Height of nests	15-35 m.	> 35 m.	10-20-35 m.	5-8 m.	> 15 m.
Roof over entry	a	a	a	a	p
Female chooses site			p	p	
Terminal hanging branch			p	p	
Isolated tree	p	p	p	a	p

TABLE 1. COMPARSIONS OF BEHAVIOR IN COURTSHIP AND NEST BUILDING (continued)

Character	Gymnostinops montezuma	Zarhynchus wagleri	Ostinops decumanus	Psarocolius angustifrons	Cacicus cela
Nests close together	p	p	p	5-10 over 100-200 m.	p
Leeward side of tree	p	p	p	a	
Base in whorl of leaf bases			p	p	
Previous year's base		p	p	p	
Materials			Slender & fine	Coarse & turgid	
Palm strips and fibers	p		p	p	p
Tendrils—vines	p	20-25 cm. long	80% at start		p
Bark strips		p	p		
Air roots			p		
Weed stalks	**p**	p			
Grass and sedge			**p**	p	
Bromeliads			Nearly all of interstices		
Lining					
Leaves	Dead & dying p	Soft leaves, fibers	Dry p	Green {Bromeliad Sedge Heliconia	Kapok cotton
Bark		p			
Collect			At distance	Near nest	
Steal loose ends	p Often	p Often	Rarely	p Often	
Nest Building					
Base of wrapped tendrils	p (knots)	p	p	p	p
Head over limb, reaches under to grasp	p	p	p	p	
Apron	p	p	p	p	
Convert to loop	p	p	p By uniting edges	p By uniting edges	p
Standing in ring	p	p	a	a	p
Work head down	p	p	(p) a	a	p
Enter by door		p	p May enter below	**p** May enter below	
Enters on wing—no pause	p	p	a Only if hurried	a	
Perches and pauses as leaves	p	p	p	p	
Female works inside	p	p	p	p	p
Building time	14-16	23-25	9-25	19-33 ad. 17-51 yg.	
Nest length	60-120 cm.	55-100 cm.	125-137 cm.	76-140 cm.	30-45 cm.
Large diameter	17-23 cm.	20 cm.	20-22 cm.	20-22 cm.	
Incubation days	@ 14	17	17-19	19-20	
Nestling days	@ 30	36	28-34 or 31-36	25-30	

p = action or article is present.
a = action or article is absent.
pa = action or article may be present or absent.
Blank means no observation is available.
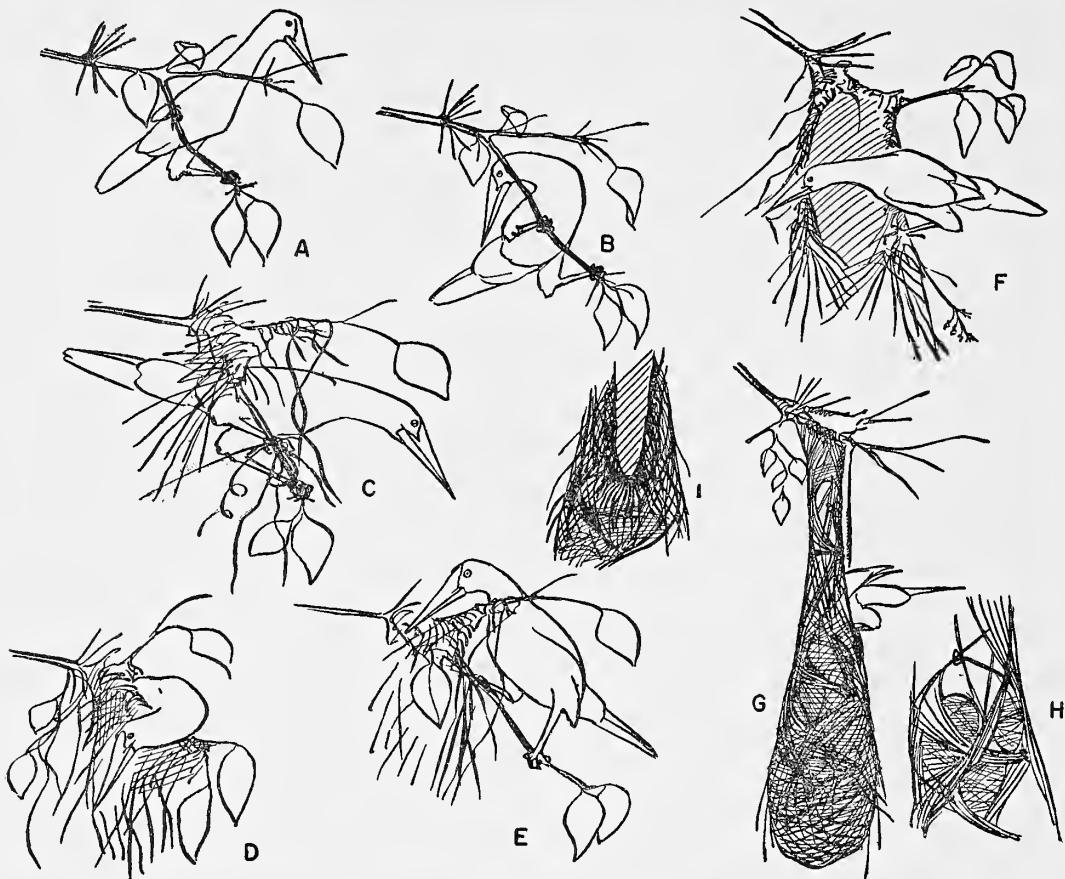
TEXT-FIG. 3. Nest-prospecting and nest-building postures. **A. & B.** Investigating possible nest site, Phase 1, at Nest 1. (Note cluster of previous year's leaf bases). **C.** Looking over valley before leaving, Phase 2, when nest base is still a ball-like snarl at the fork. **D. & E.** Reaching over and down for a loose end to pull up over and tuck, Phase 2. **F.** Perched on the hanging apron, reaching across to pull around and tuck—the first stages of closing the entrance, Phases 4 and 5. **G.** Pattern of grasses in Nest 5, with female perched in entrance feeding young. **H.** Detail of pattern of weave in the side of a nest. **I.** Detail of the weave at the base of the entrance—Nest 9.

At first (at least one day) she perches as often with both feet on the branch as with one foot down, but as the material gradually lengthens she spends more time perched on the hanging material. Later she may again perch with one foot on the branch, even after the two halves are partially joined together (see below).

Phase 4: Buldiing the Sides of the Entrance.— Now, as the female returns with fibrous material, she perches with both feet on the hanging, tangled mop. She works between her feet with her head up, pokes her load of grass into the woven material, reaches out and around, pecks, pulls out and up, brings head in, and pokes with three or four shakes of her bill; or she pecks, pulls out and around behind, and pokes in behind with a shake.

At this stage she adds a new motion: she first stuffs the large beakful of rather short material into her work; then she pushes her bill through the material, grasps a bit in the tip of her bill, pulls it back toward her, then moves it horizontally and pokes it into the weave again—with or without a short (four or five) shake. I refer to this as "horizontal peck-pull-poke." Schäfer considers this action specific to the wadding or filling (*bourrage intercalaire*).

As long as she weaves with both the peck-pull around-tuck and the horizontal peck-pull-poke, she weaves the supporting structure—the horse-shoe-shaped cross-section—with overcast edges. This part of the nest often has holes in it because the bird spends most of her time overcasting the edges. She spends less time working with
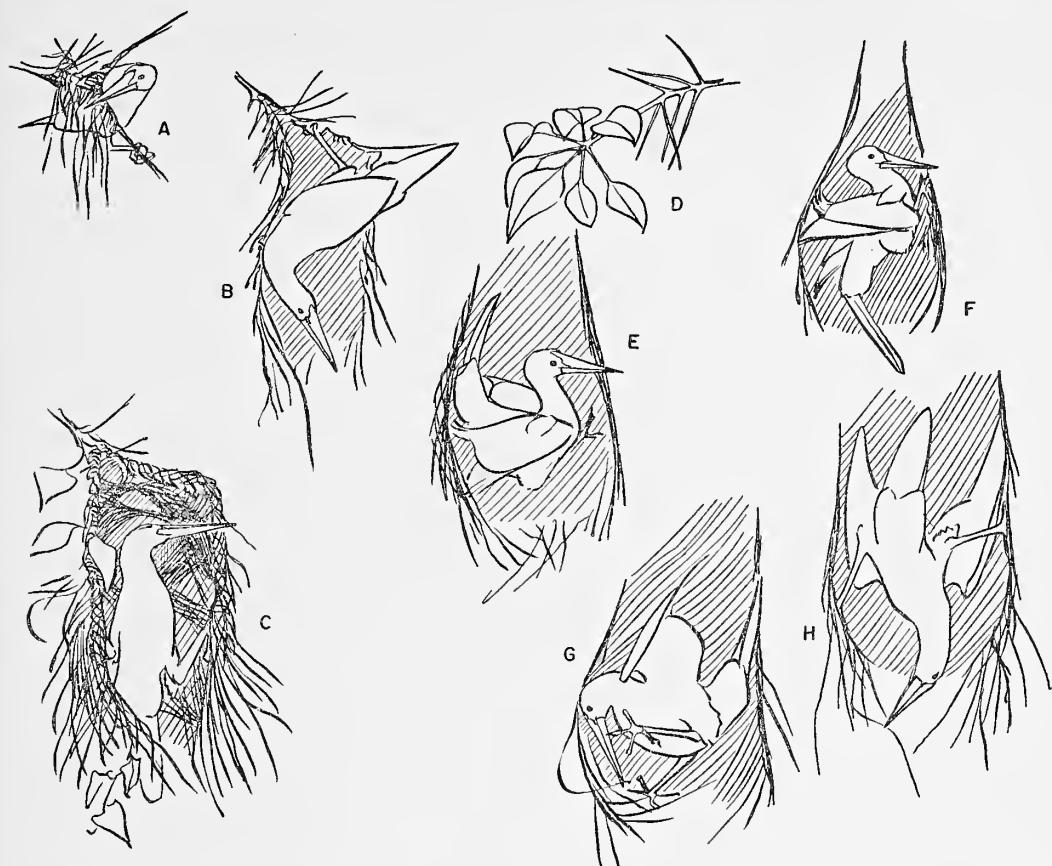
TEXT-FIG. 4. Nest-building postures. **A.** Working on the nest base, Phase 2 at Nest 1. **B.** Working on the apron, Phase 3 at Nest 9, when still perching on the branch. **C.** Perched on the two halves of the apron, Phase 5 at Nest 10, starting to work the edges together. **D.** Branch tip of *Erythrina,* showing this year's cluster of leaves and last year's shriveled leaf bases. **E. & F.** Perched inside nest, working on the nest bag below the entrance hole, Phase 6 at Nests 13 and 19. **G. & H.** Reaching below feet to pull hanging pieces in closing the bottom of the nest, Phase 7 at Nests 13, 15, 19.

the horizontal peck-pull-poke which weaves the fabric of the bag. The supports of the nest are thus straplike, tied together tightly by connectors, but they do not form an evenly woven bag (Text-fig. 3H); crudely, they resemble the braided handles of a string shopping bag. Schäfer says that *decumanus* usually works head-down (in contrast to my observations), but that *angustifrons* works on the apron head-up.

Phase 5: Closing the Base of the Entrance.— (Schäfer calls this the ring and future entrance). To start joining the two sides below the entrance, the female uses the horizontal peck-pull-poke on the material which hangs loose and frayed across the open bottom of the horseshoe-shaped sleeve, and, as Schäfer says, she uses long pieces at this stage. At first she perches on one side and takes a bit of grass from the same side, pulling

it across to poke it into the other (Text-fig. 3F). Finally, she perches with one foot on each side of the horseshoe, and works strips across from one side into the woven part on the other (Text-fig. 4C). She may work either on the outside or the inside of the sleeve, and may spend all of several visits below the entrance, working horizontally on the lower part of the structure. This transition may be seen as a gradual increase in use of the horizontal peck-pull-poke, until it is applied all around the bag and replaces the peck-pull around-tuck. She closes the gap, still using a combination of the horizontal weaving and overcasting actions, but her attempt to join the sides is not immediately successful; usually she starts to bring the two sides together about a foot above the place where they are ultimately joined. The entrance may be 30 to 45 cm. long

if she starts to close it soon after the apron is large enough for her to perch on, or it may be 60 to 90 cm. long if she continues to weave with the overcasting action. This accounts for differences in lengths of the hanging nests. Nests vary from just over two to more than four feet long (60 to 120 cm.). Schäfer emphasized that the difference in experience between young and old females may explain the observed differences in length.

When the base of the entrance is closed and the apron has become a sleeve, the female spends a long time working with the overcasting motion on the margin at the base of the entrance. At this point the pull-around is vertical. Thus she weaves a buttonhole-like stitch along the bottom of the entrance (Text-fig. 3I). Her weight, coming and going, pulls the material down, and by pulling it thus makes the dense weaving stronger where she perches to enter. Before the entrance is well sewed in, she usually still hitches up woodpecker-like to the branch to perch and look around before she flies off. Entrances are on the lee side of the nest.

Phase 6: Building the Sides of the Nest.— While she is working on the sides and supports of the nest, the female characteristically works on the inside, but often works on the outside. As soon as the bottom of the entrance is firmly closed, she does almost all her work on the inside. As far as I could see, she uses chiefly the horizontal peck-pull-poke action and brings larger beakfuls of material (on an average 30 to 60 cm. long).

As the female works inside the bag, she sits woodpecker-like (her tail may be bent up behind her in the the sleeve and occasionally her wings may be partly opened (Text-fig. 4E & F). She works four or five minutes, reaching slowly and carefully through the weave to grab a bit of fibrous material in the tip of her bill, pull it toward her, then poke it through again, often with a little shake. There is less pulling, tugging and wrapping of long pieces, and more delicate attention to detailed weaving. Also, she spends much less time, proportionately, gathering building materials at this stage.

Now she starts to add a new movement. After about every ten to fifteen horizontal weaving actions, she reaches down between her feet to peck, pull up and poke (Text-fig. 4G & H). The longer she continues to use only horizontal weaving, the longer the bag of the nest.

Where two nests are built immediately next to each other, the female may carry her weaving action across into the material of the adjacent nest, as Skutch pointed out. I observed this in

the case of nests #7 and #13 (Text-fig. 1). Skutch described how one bird, building thus into a neighbor's nest, seemed to make its own nest an additional length below the bottom of the neighbor's nest so that there was a "proper" length of bag hanging down. The two females I watched did the same. This suggests that a definite length of bag stimulates the bird to the next activity, which leads to closing the bottom. Crook's (1960) discussion of the change of stimuli which leads to changes in the building techniques used by weaver finches agrees with this.

Phase 7: Closing the Bottom.—During the building of the sides, the female perches with both feet at the same level, above or just below her bill, and works reaching ahead, beside or between her feet. In closing the bottom, she reaches way down between her feet, almost doing a somersault (Text-fig. 4G and H), grasps the long, hanging strands, pulls them up to eye-level, and weaves them into the side—pulling and poking with little or no evident shaking of her bill. As she moves around she gradually takes more and more bits from one side and weaves them into the opposite side. This closes the bottom. But because of her weight and her inefficient actions, she is not immediately successful. The stage at which she shifts to closing the bottom and her success with the cross-weaving govern the length of the hanging bag. She continues to weave horizontally, alternating work on the sides and on the bottom. Schäfer reports that young female *angustifrons* may have to try several bottoms before they succeed.

Chapman, Skutch and Schäfer commented that their birds entered the nest only through the entrance—once the entrance is formed. While building the sides, the Yellowtail usually enters and leaves by the entrance, but may often fly in and out through the bottom of the nest, even after she has started to close the bottom.

When the first strands are hooked across the bottom, the female spends much time weaving between her feet, pulling especially hard on the grass with which she is working. During this action her wings are often partly raised and her tail is pushed hard against the side of the bag (Text-fig. 4G). Her pushing movements inside and her weight as she climbs up the sides combine to enlarge the gourd-like bottom, and to pull the strands taut. Schäfer comments on the joggling and pushing inside the nest during this phase, which forms the 25 cm. diameter of the bag.

Phase 8: Lining the Nest.—My observations at one nest suggest, as do Tashian's, that the birds

use bits of leaves, chiefly erythrina, to line the nests. I could not see the motions used in forming this lining because the nest screens them. Movements visible on the outside of the bag, however, showed that the bird frequently changed her position, joggling the nest, and that her wings and tail were raised. Other birds, whose nest-molding activity has been recorded in detail, thrust the breast forward by pushing the feet back and up, and Schäfer's observations show that *decumanus* tramples the nest-lining materials (torn fragments of dried, brown leaves) while turning around and around.

This is the period of the female's receptivity to copulation.

Attentiveness to Building.—The birds build fitfully as they weave the base and may be absent for several days. Schäfer says the period lasts one to nine days, according to the level of stimulation and to the female's age. As the sides of the nest are started, they still build sporadically and may be absent for a day or two, but then work with energetic spurts of concentrated activity. Schäfer says the closing of the ring takes one to six days and that an inexperienced *angustifrons* worked 16 days and built down 1 m. before successfully closing the entrance. After the birds start to weave the hanging sleeve, they work constantly until the bottom of the nest is partly closed, which takes four to five days (Schäfer). Then they may be absent for a day or two before the bottom is brought together. Once finally started on the bottom, they work constantly until it is closed, but they may pause again before weaving the thick bottom and lining the bag which takes two to six days. Even when the heavily woven bottom is finished, the female may spend hours slowly and carefully weaving horizontally part way up the bag.

DISCUSSION

Function of the Territory.—Skutch and Chapman commented on the peculiar territory structure in the oropendolas. They were unable to establish whether a male took up a territory and defended it, and whether pairing was promiscuous or polygamous. Schäfer compares territorial behavior in *decumanus* and *angustifrons* in detail but does not comment.

Males seem to give their attention temporarily to one group of females and readily shift attention to a new group. In the Yellowtail, my observations point to isolation of males on their own defended territories, but although I watched for 35 hours at one tree with 43 nests (long enough to expect to observe frequent copulations if they were restricted to the male whose

territory included the nesting tree), I saw copulation there only twice. During the same period I saw eight copulations in trees with no nests. This suggests either (a) that the females are nesting in one particular male's territory but each is paired to a specific male whose territory may be elsewhere, or (b) that the females nest together in one male's tree by flock formation among the females without regard to sexual relations with any particular male. There may be polygamy, no pair formation or "standard" pair formation. The restriction of the term "pair formation" to those cases in which copulation takes place only with the pair partner, may not necessarily apply to these birds. Such limitations gratuitously suggest some form of propriety— which may be anthropomorphic. My notes, and Schäfer's, show a hierarchy of several males associated with a colony tree. Thus there is territory but its exclusiveness is modified. Schäfer points out the lowering of territorial "jealously" during the copulation period in *decumanus* and what appears to be complete promiscuity in both species where inferior males intrude to copulate with receptive females while the dominant male is occupied.

Chapman and Skutch suggest that groups of females establish a new nesting site and that the presence or absence of the male is unimportant; in fact, the males seem to follow groups of females. Schäfer's observations, especially of *angustifrons,* show the necessity of the territorial males' constant stimulation to arouse and carry through the females' interest in nesting.

These observations and mine lend support to Tinbergen's (1957) explanation of the function of territory; namely, the combination of a need for the male to act in a specific way recognizable by females and other males during pair formation, coupled with a need for the male to have a fixed location. The site, in the case of the oropendolas studied by Skutch and Chapman, seems to be a group of females rather than a map area. With this change in structure, it may become selectively advantageous to the species to de-emphasize the aggressive aspects of the display of the male or lower his tendency to exclude other males. Thus, the male goes through his song display to stimulate the female, but he is not necessarily bound to drive away other males, and the female does not necessarily restrict her attentions to one male or the male in whose territory she builds. I can see no way in which food enters directly into the selective advantage of territory in this case.

Closing the Ring.—The building of the entrance by the Yellowtail contrasts with that described by Skutch and Chapman for their

species. Their birds weave an apron across the fork and then, standing on the material, push an entrance through the partly woven material which then becomes a circle or loop. This loop is used as a perch, and the sleeve is woven downward from it—the bird hanging head down into the sleeve. Although they do not dwell on details, the descriptions of these authors suggest that their species use techniques of building the base and loop which are similar to those used by the True Weavers (Ploceidae) as reported by many authors (Friedmann, 1922, Ali, 1931; Grzimek, 1952; Collias, 1959; and Crook, 1960).

The techniques which Schäfer and I describe are similar, and differ from those of the weavers. While the weavers make a ring first and build the nest bag out from the ring, which becomes the mouth of the bag, *decumanus* and *angustifrons* build a hanging apron (horseshoe-shaped in cross-section) directly down from the foundation on the branches and join the free ends to form the ring and the entrance. The techniques of weavers and oropendolas resemble each other in the weaving of free-hanging ends from one side into the other, but differ in the location of the ring in forming the nest foundation, and (at least in *decumanus*) differ also in that the female oropendola works with her head at the level of her feet or above, while the male weaver works with his head down below his feet.

Skutch watched one *montezuma* after her properly formed circle was broken when her neighbor stole some loose ends. The robbed female perched with one foot on each side of the ring and in this "uncomfortable" position closed the two sides in the same way as I observed the Yellowtail to do. This suggests that the two systems may not be fundamentally different in the oropendolas.

Entering and Leaving.—Both Skutch and Chapman observed that the returning bird darts swiftly into the nest entrance as soon as it has been formed. They suggest that the fast disappearance into the bag and the long look around before leaving serve to avoid predation. In building the foundation and sides of the nest, however, the female Yellowtail perches on the outside and is conspicuously exposed. Even so, she peers around over the valley just before flying away. Also, later in the cycle, when she visits the completed nest or comes to feed the young, she perches for ten to twenty seconds with her head down inside the bag and her yellow tail hanging out conspicuously. This action must deny the significance of the fast dart

into the entrance as only to avoid predation. There may be advantage to the peering around before leaving, but it would seem that the technique of entering may be dictated as well by the bird's heavy wing-loading which exposes her to the danger of stalling as she flies up sharply to the entrance.

Techniques of Nest Building.—Herrick (1911) pointed out that the stereotyped movements used by birds to build their nests are convenient tools for the comparative study of behavior and its evolutionary aspects, yet little work has been done since. Later, Laven (1940a) repeated this suggestion. Several authors have described the nest-building activities of birds that nest on open ground, especially the non-passerine species, *e.g.*, Selous (1902) and Brock (1911) for the Lapwing, *Vanellus vanellus;* Portielje (1925) for the Cormorant, *Phalacrocorax carbo,* and (1928) for the Herring Gull, *Larus argentatus;* and Tinbergen (1931) for the Common Tern, *Sterna hirundo,* and (1936) for the Herring Gull. Several studies have shown how universal certain nest-building actions are. Although the loons, *Gavia stellata,* (Huxley, 1923) and grebes (Huxley, 1914; Selous, 1901) merely drop their nesting weeds, moss or mud on the nest edge, most birds add them with some form of tremble-shove: Cormorant (Portielje, 1925, and Kortlandt, 1940); herons (Lorenz, 1955); storks (Schüz, 1943); and perching birds, Raven, *Corvus corax* (Lorenz, 1940). Friedmann's (1922) study of the building actions of the Ploceidae was one of the very few on perching birds until the Second World War. In 1943, Nice mentioned the appearance of generalized nest-building actions in the developing behavior of young Song Sparrows, *Melospiza melodia,* and since then several authors have reported on the early appearance of these fundamental actions (Dilger, 1956; Goodwin, 1954; Kramer, 1950; Nicholai, 1956; and Schüz, 1943).

Nest-building actions, more or less modified, are used by many species as part of courtship actions, *e.g.*, Great Crested Grebe, Cormorant, herons, woodpeckers, Lapwing and other shorebirds, Alcidae and estrildid and ploceid finches. In addition, certain of the actions associated with nest building, and thus presumably primarily sexual, have been transferred to aggressive action, *e.g.*, scraping by Ringed Plover, *Charadrius hiaticula,* (Laven, 1940), and Killdeer, *Charadrius vociferus;* nestling and scraping by Collared Flycatcher, *Ficedula albicollis,* (Löhrl, 1951; Curio, 1960); and grass pulling by Herring Gulls (Tinbergen, 1951 and 1952). Moynihan (1955) argues, however, that grass pulling by Herring Gulls is not transferred from sexual

motivation, but is directly aggressive as redirected attack.

Kluijver (1949/1955) seems to have started the revival of detailed studies of nest-building techniques. He describes the building actions of the Great Reed Warbler, *Acrocephalus arundinaceus;* van Dobben (1949) describes the building actions of the Icterine Warbler, *Hippolias icterina* and Chaffinch, *Fringilla coelebs;* and Kramer (1950) describes the nest-building actions of the Red-backed Shrike, *Lanius collurio.*

Kluijver, van Dobben and Kramer define the fundamental actions of nest building in passerine birds as three: (1) nestling—the bird presses its breast down into the nest-cup, usually with bill and tail pointed upward; (2) trampling—the bird presses its breast to the bottom of the nest-cup and kicks vigorously and repeatedly with each leg, backward and upward (3) pecking, tugging and tucking—the bird reaches forward and grasps nest material, pulls it one way or the other, and tucks it into the nest again. These actions are the same as Herrick (1911) describes for the nest building of the American Robin, *Turdus migratorius,* Red-eyed Vireo, *Vireo olivaceus,* and Baltimore Oriole, *Icterus galbula.* Additional detailed studies of a number of passerine species show how widely distributed these actions are: Sylviidae—Lesser Whitethroat, *Sylvia curruca,* and Blackcap, *Sylvia atricapilla,* Dechert (1955), Icterine Warbler, van Dobben (1949); and Great Reed Warbler, Kluijver (1949/1955); Paridae—Long-tailed Tit, *Aegithalos caudatus,* Maxse (1951), Tinbergen (1953b), and Bearded Tit, *Panurus biarmicus,* Koenig (1952); Sittidae—European Nuthatch, *Sitta europaea,* Löhrl (1958); Ploceidae—Baya, Ali (1931), and Village Weaver, Grzimek (1952), and other weavers, Crook (1960); Estrildidae of several species, Kunkel (1959); Turdidae—European Blackbird, *Turdus merula,* E. and I. Messmer (1956); Muscicapidae, Löhrl (1951), Curio (1960); Fringillidae—Chaffinch, van Dobben (1949), Marler (1956); and Emberizidae—Song Sparrow, Nice (1943).

All these studies show that the movements used by passerine birds in placing nest material and forming the nest-cup are uniform and widespread, but as Dechert (1955) illustrated, the important thing is the sequence of these actions, the materials used and how they are used. Her study of the Lesser Whitethroat and Blackcap showed that these closely related species used nearly identical actions but different materials, and that they used the actions in different proportions, thus creating quite different nests. A further illustration of the importance of the material chosen is given by Lorenz (personal communication) who, when first keeping some Red-billed Weaverbirds, *Quelea quelea,* discovered that they were unable to build their huge nests because the grass native to Germany did not "stick." He obtained some of the grass the birds use in their native Africa and found that the leaves of this grass are "retrorsely scabrous" on their margins (have small tooth-like spines on their edges), causing the leaves to cling together. Ali (1931) realized the importance of the scabrous margins of rice leaves in the nest building of the Baya. Schäfer's study also shows the importance of different nesting materials in similar species, but his study also shows use of different actions (in anchoring the base). Nickell, (1958) examined nesting materials and nest types of 169 species of eastern North American species.

In a number of families scattered among the perching birds, some of the generalized actions have atrophied and some actions have been added to the basic repertory. The estrildid finches (Kunkel, 1959) built their messy, domed nests with the following actions: (1) the bird, standing in the middle of its nest, grabs material with its bill and pushes it away, or it may simply push at the wall and roof of the nest with its head; (2) the bird grasps material and pulls sideways, either to the left or to the right; (3) the bird pulls material directly toward itself into the cup. In these actions, the birds have lost certain of the basic behavior sequences and their nests seem to reflect this.

It is interesting, in terms of the former classification of the estrildid finches with the ploceid finches (Steiner, 1955), that they share two unusual nest-building actions: (1) termination (Crook, 1960)—a grass stalk held in the beak is moved by a rotating motion of the bill until it is held at one end; (2) to stretch the building material and form the pocket-like nest, the builder pushes against the walls with its head or bill.

The highest development in nest building, nearly all authors agree, occurs in two families —the Old World True Weaver Finches (Ploceidae) and the New World blackbirds, troupials and orioles (Icteridae). Ploceids such as the Red-billed Weaverbird studied by Friedmann (1922), the Baya described by Ali (1931), the Village Weaver described by Grzimek (1952) and studied and photographed by Collias (1959), and the species discussed by Crook (1960), use additional actions to weave and tie knots in their material in order to fasten it to the foundation branches. According to Friedmann (1922) and Crook (1960), the True Weavers take a fiber in the bill, hold it at the end,

place it on a branch (sometimes holding it with the foot), then take one end of the fiber and push it to the far side of the branch. Reaching around the other side, they take the strand and tuck it under the part they are standing on, then pull taut the knot that has been made. The fiber is repeatedly drawn round and round, each time being inserted within the previous loop. The end may also be looped in and out through the already-woven fabric.

Collias (1959) describes "four basic mechanisms in working a grass strip into its nest. He tends (1) to bend the strip about some object, either a twig, another grass strip, or his own leg; (2) to double a strip back on itself; (3) to alternate the direction in which he winds the strip about objects such as twigs or other grass strips; and (4) to poke and pull a strip through holes, normally the interstices of the nest materials. It is in the possession of mechanisms (3) and (4) that a true weaver (Subfamily Ploceinae) differs from other weaverbirds. . . The end of a strip is often looped back on itself in such a way that pulling on the strip tightens its attachments. This is essentially a hitch type of knot. Knots of other types than the hitch are rare." In this specific treatment of an individual fiber, the action of these birds differs from that of many Icteridae. They tuck a bill full of fibers into the nest material and then may ignore them until dealt with again "by accident."

In the ploceid finches, the foundation of the nest is made by forming a loop on which the bird stands and which it uses as an entrance from which to build the sleeve that will become the nest bag. The caciques and oropendolas studied by Skutch and Chapman resemble the True Weaver Finches in building a similar loop. These authors also suggest that the birds wind the strands around the branches to form the foundation of the nest. However, my study of the Yellowtail, and Schäfer's, show that such behavior is not characteristic of *decumanus* and *angustifrons*.

The New World orioles have specific actions peculiar to themselves which are slight modifications of the generalized ones of most perching birds: pecking, pulling around and tucking (Herrick, 1911, Baltimore Oriole). Herrick showed that after the nest bag was constructed, the Baltimore Oriole also used the standard trampling, nest-molding technique. The fact that the enormous and complex nest of the Yellowtail is built by simple actions which are used by other species to make much simpler nests, points to the generalization that variation is built out of specializations of a few fundamental "inventions."

To emphasize this, Selous (1902) and later Kramer (1950) pointed out that the scraping actions of plovers and sandpipers, gulls and terns, are homologous with the trampling actions of perching birds making their cup-shaped nests. Similar trampling actions are found among a number of the Laro-limicolae: Lapwing, Selous (1902), Brock (1911), Rinkel (1940) and Laven (1941); Turnstone, *Arenaria interpres,* Bergman (1946); Northern (Red - necked) Phalarope, *Phalaropus lobatus,* Tinbergen (1935); Common Tern, Tinbergen (1931); Caspian Tern, *Hydroprogne caspia* or *tschegrava,* Bergman (1953); and Herring Gull, Tinbergen (1936). Furthermore, these studies show that there are other nest-building actions in gulls and terns (and my own studies show that the same is true in sandpipers, *Calidris bairdii,* and plovers, *Charadrius vociferus* and *Ch. melodus,* similar to those of perching birds. When sitting on its scrape, the bird picks up material and either drops it over the shoulder or pulls it immediately in front of itself and drops it. These actions are identical to the sideways pulling or the peck-pull around-tuck action of perching birds. The big difference, of course, is in the choice of nest-building material, the uniformity of treatment and concentration given to the material. Shorebirds and gulls either use no material, cast the material aside, or do not pursue the treatment to a final resting place.

Many small perching birds may spend two or three days building; the Red-eyed Vireo spends approximately five. The Yellowtail may spend three to five weeks. A Killdeer may spend two to three weeks scraping, and then continue for another three weeks throwing nest material over its shoulder, or pecking, pulling and dropping material on the edge of the nest after the eggs have been laid until they hatch. The bird usually kicks with its feet five to ten times in the trampling movements each time it settles on the nest. In the Piping Plover the persistence of this action is functional. It is used to uncover eggs that have been buried by blowing sand. Similar actions are used to uncover buried eggs by the Kentish Plover, *Charadrius alexandrinus,* and the Little Ringed Plover, *Charadrius dubius,* (Walters, 1956), and by Kittlitz's Sandplover, *Charadrius pecuarius,* (Hall, 1958), which regularly covers its eggs when frightened from them.

Clearly, the type of action and the amount of time spent on the action does not control the end product. But there seems, in fact, to be a sequence in the intensity of attention paid to the nesting material from (a) the very careless handling by shorebirds and gulls through (b)

the sloppy work of the estrildid finches, to (c) the situation found in most perching birds, and finally (d) to the True Weavers and icterids. In the evolution of nest building (which is at least in part independent of the evolution of those factors used in classification), similar motions have been applied to different types of material, and a change has been made according to differences in the "plan in mind" and perseverance to that plan: specialized actions added, and new reactions appearing to specific building situations. The difference is not in the motion (the tool) but in the central nervous system, which in turn is modified, within limits, by changes in environment which influence the living bird (see especially the differences in the nest building of young and old female *angustifrons* studied by Schäfer).

Stereotyped Behavior and Brain Structure.—In considering the modification of behavior patterns in evolution and according to experience of the individual organism, the basic difference in brain structure between birds and mammals must be taken into account, as described by Cobb (1960). In birds, the basal area of the forebrain, the *corpus striatum,* has been greatly enlarged. This is the area associated with quick, complex physical co-ordination. In contrast, the roof of the forebrain in mammals has been developed—an area whose specialization has tended toward associations developed during the experience of the individual.

The impression of bird behavior is of stereotyped responses (consistent and efficient) that are uniform as they occur, but whose occurrence is modifiable between species and according to experience of the individual bird. Certain stimuli or events change the bird's instructions and its behavior shifts. When watching the Yellowtail construct its nest—operating steadily and mechanically with a smooth, weaving action for a period of time, and then shifting over to a new system of weaving—I was strongly reminded of the control on an automatic loom by a card. The machine's motions—and the bird's—do not have the ability to change the card. The ability to change the card must, in a very crude way, be the organism's ability to learn and associate. The bird's actions are efficient in its present circumstances and, through evolution, suitable to its environment. During the bird's life, it seems that inherited material is as if carded and in units, and during maturation the bird "learns" what conditions, stimuli or parts of the environment are suitable for the expression of that inborn activity. The nest building of the Yellowtail is an illustration of the complex train of activity patterns that is changed to another

complex train by a stimulus, rather than an illustration of a series of simple actions built up by association into complex trains, as seems to be the product of much mammalian learning.

But this illustration does not clarify the crux of the questions presented by the shifts in nest-building behavior by the Yellowtail. What combination of "things" leads to the decision to change the "card?" How does the bird treat inconsistent information upon which it must base its decision? For example, the behavior of a bird whose nest has been partly destroyed by the robbing of nest-building material by its neighbor. There must be a "look" (Thorpe, 1956; Crook, 1960; ? *Gestalt*) about the material and the state of construction which influences the sequence of activities that the bird follows. This hypothesis is supported by several natural tests resulting when several males work at the same nest (Crook, 1960). The bird's actions are neither guided exclusively as if by the unravelling of a string, as seem to be the activities of an insect, nor yet with the gradual brick-by-brick building of the association of learned actions into a whole, as may be the case with much mammalian development.

Summary

1. Yellowtails nest in colonies, 2-43 nests in the Arima Valley, chiefly in *Erythrina micropteryx,* an introduced shade tree towering over the cocoa, coffee and banana tree plantations.

2. A dominant male defends two or three neighboring trees but allows intrusion of subordinate males if the intruder does not display. Males have a territorial and a sexual song.

3. Males hold territories in nestless trees, and females copulate with males other than the dominant male of the colony tree.

4. Groups of females within a colony, nest according to a schedule independent of other groups.

5. Nest-building material is collected in valley bottoms away from the colony tree; it is chiefly grass, sedge and thin vines. The building material averages 30-45 cm. when the female starts the base, 60-100 cm. when building the supports and sides of the entrance, 30-45 cm. in weaving the bag, and 100-150 cm. when closing the bottom. The nest appears to be lined with dried leaves.

6. Detailed observations of nest-building technique show that a few simple movements are used and that the fibrous strips are dealt with by chance—not woven in individually. Actions are:

(a) Push billful of material into the work, reach over and grasp any end, pull around and tug, tuck in with tremble-shove. The female may perch on the branch or on the apron that she in making when using this technique;

(b) Push billful into the work, push bill through and grasp end, pull out and move to the side, tuck with a shake. The female perches woodpecker-like on the side on the nest;

(c) When closing the entrance, the female weaves across the two free edges, then overcasts the edges to bind the entrance with a buttonhole-like stitch;

(d) She uses chiefly the horizontal movements in making the bag, whose length seems to be measured by distance below the entrance. In closing the bottom, she reaches down between her feet to peck, pull up and poke.

7. The bird's attentiveness to nest building varies, being least at the start, strongest when building the sides of the nest, and interrupted before the bottom is closed and the nest lined.

8. Discussion:

(a) Territory in Yellowtails suggests purely courtship function. Copulation appears to be promiscuous;

(b) Closing the entrance and weaving the sides of the nest, as observed by Schäfer and myself, use different techniques than have been described so far;

(c) It is not clear why females hesitate on the nest entrance when entering and leaving;

(d) A review of nest-building techniques shows that three fundamental movements are widespread even among non-nest builders such as gulls and plovers. To these movements some groups have added actions by which they construct sloppy or elegant nests. The fine nests of the ploceid weaver finches are based on persistent individual attentions which tie knots in the fibers. Among the Icteridae, the fiber gets attention by accident, once it has been pushed into the work. Closeness of weave and security of attachment result from persistent repetition of actions.

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7

Further Observations on the Pilot Whale in Captivity[1]

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(Plates I & II)

INTRODUCTION

RECORDS on the behavior of a captive Atlantic pilot whale, *Globicephala macroryncha* Gray (Kritzler, 1952), and of captive Pacific pilot whales, *Globicephala scammonii* Cope (Brown, 1960), have shown that these delphinids generally adapt readily to confinement in large aquaria.

At Marineland of the Pacific, Marineland, California, Pacific pilot whales are exhibited with striped dolphins, *Lagenorhynchus obliquidens* Gill, in a circular tank 80 feet in diameter and 19 feet deep. Glass windows placed in three levels of corridors permit observations of what transpires beneath the surface. Observation of surface activity can be made from a "top deck" area, where seating facilities are provided.

Prior to January, 1959, the exhibit consisted of two female pilot whales and four striped dolphins (Brown, 1960). This paper describes the capture of a male pilot whale and the activity observed upon its introduction into the tank. An account of the sickness and death of a female pilot whale, including findings at necropsy, is given. The behavior of the male pilot whale at the time of this death is also described. Also presented are remarks on laryngeal withdrawal in certain odontocetes.

BEHAVIOR DURING CAPTURE

On January 21, 1959, the Marineland collecting vessel, *Geronimo*, while operating in the Catalina Channel, California, encountered a very diffuse school of approximately 40 pilot whales. Several distinct pods were involved, some being almost a mile apart. Family groups were seen in which a male could be observed swimming with mother and young.

The men maneuvered their vessel close to what appeared to be a family group, consisting of a female, a calf and a larger male. The collector had the opportunity of rapidly snaring the latter animal, which for the first 35 minutes after becoming ensnared, towed the *Geronimo* around in large circles. The animal was quickly brought alongside the boat by winching in the nylon lead rope. No sounds were heard coming from him during any of these procedures, and while still attached to the line his dives consumed about five minutes. The animal had a tendency to dive and then rest at the end of the dive, leaving the line quite slack. The large size of the pilot whale made it impossible to lift him aboard, so, to effect his transport to Marineland, a deflated 20-foot rubber life raft was pulled beneath the animal, quickly inflated, and thus he was safely secured during the return trip to port.

The animal was measured and found to be 17 feet 3 inches long; his weight was estimated to be about 3,000 pounds.

INTRODUCTION INTO THE EXHIBIT

The pilot whale made no movements in the raft during the return journey or while he was hoisted into the exhibit tank. Upon being released he quickly dived and began to swim slowly in a head down position, only inches from the floor of the tank. After being submerged for five minutes he surfaced to blow, and then again resumed the head down position, which he maintained for several hours, interrupted only by excursions to the surface to breathe.

At this time the female pilot whales appeared to show fear and swam rapidly together around the periphery of the tank, accompanied by the

striped dolphins which also appeared to show apprehension at the presence of the new arrival. Several hours later, toward the end of the day, the female whales commenced to rub their flipper tips against the male. The females were also seen to butt the melons of their heads against the larger melon of the male.

By the following morning the animals were quite familiar with one another and in the ensuing weeks, between feedings, spent their time swimming (Plate I, Fig. 1) or lying together in close formation on the surface in what appeared to be a resting position.

Feeding the New Arrival

Inducing newly arrived cetaceans to accept nourishment in capitivity is often difficult, owing to the stresses of capture, unusual confines of captive environment and the type of food the animal is expected to consume.

Inanition results rapidly in emaciation with most cetaceans. Pilot whales, probably as a result of their less active behavior, seem to withstand prolonged fasting with far less weight loss than the small delphinids (Brown, *et al.,* 1960; Brown & Norris, 1956). The first pilot whale captured by Marineland in 1957 responded to forced feeding on its eighth day in captivity (Brown, 1960) while the other female commenced to accept dead squid voluntarily after 14 days of fasting. No major loss of body weight occurred in either case.

The first attempt to feed the new pilot whale was made six days after his introduction into the tank; this was effected each evening by throwing large quantities of squid into the water. The active feeding behavior demonstrated by the other animals would, we hoped, initiate a favorable response in the new arrival. This technique proved successful, and on February 1 he began to feed and thereafter regularly accepted 100 pounds of squid each day.

The rapidity with which *Globicephala* usually adapts to captivity has already been discussed (see Kritzler, 1952, and Brown, 1960). The male pilot whale also quickly responded to the attendant's summons and within four weeks of his capture learned to lunge half of his body clear of the water to accept food from his trainer's hand.

It is remarkable that what must have been the animal's well established behavior pattern did not offer more resistance to such major environmental change. It is conceivable that the presence of the female pilot whales already established in the exhibit contributed largely to the adult animal's remarkably rapid integration into the group.

Sexual Behavior

Sexual behavior among the pilot whales in Marineland of the Pacific has been seen sporadically throughout the spring and winter months. The first of the following observations was made only 25 days after the male's admission into the tank.

February 15, 8:00 a.m. Both female pilot whales were observed swimming around and rubbing against the ventral surface of male's body. After several minutes of this activity the three animals swam almost to the floor of the tank and commenced to butt their heads together with great force. The larger female moved away and began to rub her genital opening on the floor of the tank. The smaller female and the male commenced to slowly swim together, the smaller animal swimming upside down, in a position immediately under and considerably forward of the male. In this position she was seen to arch her body and vigorously rub her genital opening between the flippers of the larger animal. At this time the male extruded its penis, and when the female moved back to a position where her ventral surface approximated his, several attempts at intromission were made. Despite the female's apparent sexual receptiveness, however, penetration was not achieved.

April 1, 9:45 a.m. This morning a loud creaking sound was heard coming from the circular tank; investigation revealed the large pilot whale very active, rubbing himself against the females. The vocalization emanated from the large whale and was not accompanied by any emission of air. The sounds produced were similar to the creaking of a rusty hinge. This activity appeared to disturb the striped dolphins which were rapidly swimming around the tank in close formation. The glans penis was protruding from the male's genital opening at this time.

April 17, 10:00 a.m. The large female was swimming against and rubbing her genital opening on the ventral surface of the male. The striped dolphins again appeared very active and were also seen to rub against the male pilot whale. The two larger animals then sank to floor of tank and upon confronting each other some 30 feet apart swam at each other, butting the melons of their heads together with great force. On several occasions the smaller female through force of impact was thrust backward through the water several feet; the whip-like crack produced by these collisions could be clearly heard outside the tank. After indulging in this behavior several minutes, the male had an erection, and although the female drifted passively in the water and appeared receptive, many attempts at intromission again proved unsuccessful.

October 28, 7:30 a.m. This morning the smaller female was observed rubbing the ventral surface of her body against male's and trailing her flippers and dorsal fin over the larger animal's genital opening. After two or three minutes of this play, the male extruded about 18 inches of his penis and tried to effect intromission. Penetration occurred briefly, whereupon the male returned to a resting position on the surface, and was eventually joined by the female.

November 7, 11:30 a.m. The male pilot whale was swimming around tank with his penis extruded about twelve inches. The smaller female forcibly butted him on his side and then assumed the position noted on February 15, 1959. Intromission was again attempted.

November 14, 9:30 a.m. There was considerably activity in the whale tank this morning. Both female pilot whales were rubbing against male, who maintained a head down position. The animals were extremely vocal and produced a bleating or crying sound and a loud buzzing noise, which had not been heard before. These vocalizations were not accompanied by any emission of air from the animal's blowholes.

At 10:30 a.m. diver G. McLaughlin reported the male lying on his back at the surface with his penis extruded about 24 inches.

Other behavior of probable sexual significance has been observed many times in both male and female pilot whales. McBride & Hebb (1948) recorded similar behavior in male *Tursiops* while Tavolga & Essapian, (1957) described unpaired female *Tursiops* engaged in unusual activities of a sexual nature.

The male pilot whale is often observed rubbing his genital opening on the floor of the tank and sometimes on these occasions the animal utilizes a piece of stone; by means of body movements he attempts to rub this against the wall of the genital orifice or the glans penis, which is usually extruded at this time. The females also employ the tank floor in a similar manner. The diving ladder has been rubbed by the smaller whales so violently it has become loosened at its mountings.

Brown & Norris (1956) record sexual stimulation of male *Tursiops* by underwater petting. On one occasion a diver while swimming with the male pilot whale and patting his sides elicited an identical response; the male extruded his penis and moved towards the man.

Tavolga & Essapian (1957) have described the sexual behavior of the bottlenosed dolphin, *Tursiops truncatus* Montagu, and they state that the dominant role during courtship is as-

sumed by the male. The observations at Marineland on interspecific mating activity between female *Lagenorhynchus* and male *Tursiops* (Brown & Norris, 1956) and more recently between *Globicephala* are contrary to those described in *Tursiops* by the above authors. Observations made at Marineland generally show the female to be responsible for the initiation of precopulatory behavior.

It would appear that the wide range of sexual behavior recorded in male *Tursiops* by McBride & Hebb (1948) and Brown & Norris (1956) is not so apparent in *Globicephala*, but it must also be noted that this statement is made after observing only one captive adult male. It is possible that younger males demonstrate a broader field of sexual proclivity.

Observations on the mating activity of *Tursiops truncatus* show that little difficulty is experienced by these smaller active animals in effecting penetration. An individual upon producing an erection is able to swing the penis around in a half circle and thus can achieve intromission with an approach from either side, and by swinging on its back under the female is able to contrive intromission by a powerful vertical flexure of its body.

The male pilot whale appears to lack this underwater dexterity, and the females seem to play the major role in precopulatory body positioning. Before erection, the male's penis is enclosed within the genital sheath. When fully extended it is about 24 inches long and approximately six inches in diameter at its base. The shaft tapers to an apex surmounted by a vermiform glans some four inches long. Unlike that of *Tursiops* the penis is not rigid but flexuous, upon extension its contortions giving the false impression of independent movement. During the several attempted and one successful intromission, strong pelvic thrusts were seen.

AGGRESSIVE BEHAVIOR

In a previous paper (Brown, 1960), aggressive behavior in a female pilot whale after months of solitary confinement was recorded. After being transferred to a tank with another whale, these aggressive actions ceased. Except for one incident, to be discussed later, the male has not directed aggressive behavior towards any man, and has allowed divers to grasp his flippers or dorsal fin as he swam around the tank. This was stopped after the small female made attempts to ram and bite the man involved.

INTERSPECIFIC RELATIONSHIP AND PLAY

Schools of *Globicephala* and *Lagenorhynchus* are commonly seen swimming and feeding to-

gether in the Catalina Channel. In February, 1957, during the capture of a pilot whale, several striped dolphins accompanied the snared whale to within a few feet of the hull of the *Geronimo*.

Interspecific behavior has also been seen in the circular tank. Of particular interest is the association between a female whale and a female dolphin. This first became apparent during the spring of 1960 when they spent many days playing together, their favorite sport being to catch the air emitted from each other's blowhole. A variation of this play took place below the water-inlet jets where each animal in turn released air into the current.

Behavior of a possible homosexual nature has occurred between this pair; the dolphin nuzzled the genital opening of the whale, which then did the same to her companion.

On occasion the dolphins "tease" the pilot whales by biting their flukes. At this writing, the male is subject to this treatment, and he is seen to pursue the agile dolphins, who easily evade his rushes.

The diver's hose provides a constant source of interest to the whales, who loop the hose around their pectoral flippers and rub it with their bodies. On one occasion a man wearing a Desco mask was pulled around the tank for several minutes by the male, who seized the airline in his mouth.

Sickness and Death of a Pilot Whale

The large female pilot whale had lived at Marineland since January, 1957. During the initial months of capitivity she swallowed a rubber innertube, but after oral administration of mineral oil, the tube was regurgitated (Brown, 1960). Following this incident, the animal maintained good health until inception of the fatal sickness now to be described.

On March 2, 1960, symptoms of a gastroenteric disorder became apparent and vomiting occurred regularly after feeding. This made oral medication difficult. However, some mineral oil given in squid was retained. The animal showed no other abnormality and continued swimming activity around the tank.

March 3. The whale's condition not improved, emesis occurs after eating even small quantities of food. Attempts at medication unsuccessful. Mineral oil and kaopectate regurgitated almost immediately upon administration.

March 4. Still avidly accepts food, all of which is lost shortly after ingestion. Today quite inactive between attempted feedings and lies on surface with eyes closed.

4:30 p.m. The antispasmodic, methyl - atropine - nitrate (Metropine), given in food and apparently retained. An additional feeding at 5:00 p.m. induced vomition. Metropine again given in food at 12:00 a.m.; air and cloudy fluid expelled at 12:15 a.m.

March 5. 9:00 a.m. This morning general condition seems improved, animal active and swimming with other whales. At 9:30 a.m., Metropine given in food; some loss of fluid and discharge of air seen shortly after feeding. Animal retained all of food given during remainder of day. Apart from oral air and fluid loss, behavior quite normal.

March 6. Animal vomited during the night; considerable quantities of predigested food found floating in center of tank. Refused to swim to the feeding platform and spent the day lying on the surface with eyes closed, occasionally sounding to the floor of the tank.

March 7. The whale's condition remains unchanged. At 9:45 a.m. vomits cloudy fluid, and at 12:15 a.m. seen slowly swimming with male, eyes closed; At this time vocalized several times, making high pitched squeals which were accompanied by air emissions from blowhole.

At 2:00 p.m. returned to surface and stayed in same position for remainder of the day.

March 8. 4:00 a.m. Female lying with other whales at the surface of the tank, respiration rapid and shallow. This was the last observation made prior to death.

Behavior of the Male Pilot Whale

At 5:30 a.m. on March 8, the male pilot whale was first seen transporting the dead female to and from the surface by grasping her flipper in his mouth (Plate 1, Fig. 2). He carried her in this fashion for the next five hours. An erection occurred at 8:15 a.m., and on several

occasions he effected intromission with the dead animal. A diver entered the tank at 8:45 a.m. and endeavored to pass a rope around the female's tail. On seeing this, the male momentarily released his burden and tried to strike the man with his head. To entice the male to leave the dead animal, squid was thrown into the water, but he ignored this, seized the female and continued to carry her around the tank. Another diver entered the water, and the whale became more active. Swimming at great speed around the tank, he emitted bleating sounds and recommenced copulation with the dead female. The other female at this time began to vocalize and tried to push a diver with her head.

While endeavoring to evade the divers, the big male dropped the dead animal, which lodged between the rocks cemented to the floor of the tank. He then seized the caudal peduncle in his mouth and again succeeded in lifting the body to the surface, where he changed his hold firstly to the dorsal fin and then the flipper. In recovering the body he displaced several rocks; one large boulder weighing at least 700 pounds was propelled completely across the bottom of the tank. At 9:45 a.m. the diver finally succeeded in passing a line around the dead female's tail. The male then offered little resistance to her removal from the tank, and shortly thereafter accepted food in a normal way.

Our collectors have seen behavior of a similar nature in wild pilot whales, and report two cases of female whales supporting dead young. Several authors (see McBride & Hebb, 1948, Moore, 1953, and Hubbs 1953) have also recorded such actions in *Tursiops*.

While these mother-young relationships are not beyond interpretation, the behavior of the male pilot whale is difficult to translate. The complex social behavior of this species and the environmental restrictions of captivity without doubt furnished behavioral stimuli at this time.

NECROPSY

The dead female pilot whale had increased 23 inches in total length during the three years and two months she had been in captivity and weighed 1,360 pounds. Postmortem examination was performed on the day of death by veterinary pathologists of the Los Angeles County Livestock Department. Necropsy showed chronic enteritis. Submucosal hemorrhages with petechiae up to 3 mm. in size were found throughout the entire intestinal tract (Plate II, Fig. 3). Further investigation however, revealed laryngeal occlusion as the primary cause of death.

The following is an excerpt from the pathologist's report: "When the whale's head was totally severed from the body, a piece of rock fell to the floor, its origin unknown at that time. I approached the severed head from its posterior aspect and proceeded to dissect the remaining part of the trachea, larynx and esophagus. I was able to enter my hand into the pharyngeal area. By grasping the elongated epiglottis and arytenoid structures, then depressing and retracting, I was able to force this anterior part of the larynx out of the pharyngeal chamber. Further traction on the larynx with one hand and incision of the ventral attaching structure with the other hand resulted in my freeing the aforementioned structures.

"Dissection and examination of these structures revealed a well defined localized lesion of the mucous membrane on the floor and partly on the side walls of the larynx in the region of the thyroid cartilage.

"This lesion was approximately 5 cm. long, extended up each side wall about 3 cm. at its longest points. It was irregular in form but well demarcated. The pathological change of the mucous membrane was that of passive congestion, and edema not to the point of macroscopic necrosis. It was evident this lesion was due to pressure of the rock. Thorough examination of the esophagus, pharynx and trachea revealed no gross lesions."

DISCUSSION

During the months preceding the death of the large female, the whales were often seen mouthing fragments of stone separated from the reefs on the floor of the tank. The female pilot whale seemed particularly prone to this activity and was frequently seen to ingest, and then expel, the stone involved.

The fatal consequences of this behavior were revealed by the pathology just described, and it is evident that laryngeal occlusion induced by inspiration of a stone was the primary cause of death. It is assumed that the enteric lesions were secondary in this case.

The etiologic implications are apparent. It is quite plain that the stone gained access through the glottis into the aryteno-epiglottid tube, after entry into the palatopharyngeal region via the mouth. Oral entry was supported by subsequent investigation, which showed the stone too large to pass the bony nares of the skull (Plate II, Fig. 4). It is not illogical to assume that vomition occurred after the stone had been swallowed; during emesis, and involuntary retraction of the aryteno-epiglottid tube, the stone passed into the dilated sphincter of the naso-pharynx. Reinsertion of the tube and respiratory action

caused its migration into the laryngeal structure.

Since the death of the pilot whale, laryngeal retraction has been recorded in a male bottle-nose dolphin. This was observed while treating a lesion in the commisure of the animal's mouth. While his jaws were being forcibly held apart, he convulsed and vomited. When the animal's jaws were released, he violently exhaled and expelled vomitus through his blowhole.

It is evident that the opening of the mouth withdrew the larnyx from the nasal cavity; the enforced withdrawal prevented respiration, inducing convulsion and regurgitation. Vomitus then entered the vacated nasopharynx. Upon allowing the mouth to close, the aryteno-epiglottid tube reentered the narial cavity. The powerful exhalation cleared the nasal passage. It would then appear that on full expansion of the jaws the tube is retracted by action of the throat muscles connected to the hyoid bone.

The ability to disengage the larynx from the narial cavity by full expansion of the jaws is perhaps possessed by all odontocete whales, and possibly facilitates the passage of large items of food through the esophagus.

ACKNOWLEDGEMENTS

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EXPLANATION OF THE PLATES

PLATE I

FIG. 1. Male pilot whale accompanied by females in the circular tank, Marineland of the Pacific. (Photograph by Peter Stackpole).

FIG. 2. Male pilot whale carrying dead female in circular tank, Marineland of the Pacific. (Photograph by Robert Vanderhoof).

PLATE II

FIG. 3. Opened lower intestine of pilot whale, showing enteritis and submucosal hemorrhage. (Photograph by J. Courtland Beazie).

FIG. 4. Skull of pilot whale demonstrating the size of stone in relation to the bony nares. (Photograph by J. Courtland Beazie).
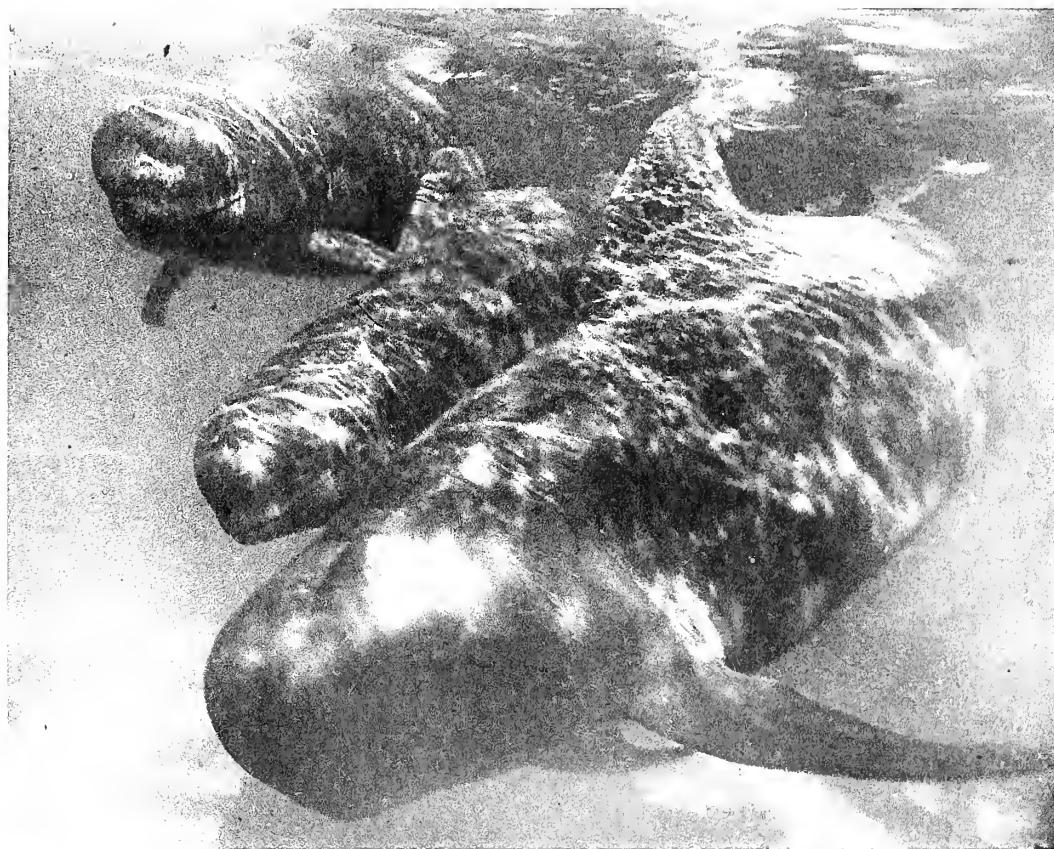
FIG. 1

FIG. 2

FURTHER OBSERVATIONS ON THE PILOT WHALE IN CAPTIVITY

FIG. 3

FIG. 4

FURTHER OBSERVATIONS ON THE PILOT WHALE IN CAPTIVITY

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Contents

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A Field Study of the Black and White Manakin, *Manacus manacus*, in Trinidad[1,2]

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(Text-figures 1-21)

Introduction

THE BLACK AND WHITE Manakin (*Manacus manacus*) is one of the commonest forest birds in Trinidad. It is also one of the easiest to study in the field, and it was this fact, combined with the outstanding interest of its communal courtship displays, that led me to devote much of my time to it during 4½ years' residence in the Arima Valley, the site of the New York Zoological Society's Tropical Field Station in the center of the Northern Range of Trinidad (Text-fig. 1).

It is a small, stockily built bird, with short wings and relatively long, strong legs (Text-fig. 2). The sexes differ markedly, the male being black and white and the female olive-green; the legs are orange in both sexes. Though it occurs in forest of all kinds, it probably reaches its greatest abundance in secondary forest. Like other manakins, it subsists largely on fruit which it takes in flight. It bathes in shallow streams, and drinks occasionally from streams but usually from water collected in the leaves and bracts of plants. Though it will feed on occasion in the tops of lofty trees, most of its life is spent within 25 feet of the ground. In particular, it nests only a few feet above the ground, and displays on and within a few inches of the forest floor. It is communal in its courtship; each male displays at a cleared "court" on the forest floor within a few yards, or even a few feet, of his neighbors. Groups of courts constitute "display grounds," which are used year after year. The

females visit the display grounds to mate. No pairs are formed, and the male takes no part in the nesting.

One other member of the family occurs in Trinidad, the Golden-headed Manakin (*Pipra erythrocephala*). Both occur in the same habitats and have largely the same feeding and nesting habits. The Golden-headed Manakin, however, displays 25 feet or more up in the trees, and also tends to feed and nest higher than the Black and White Manakin, so that, although it is even more abundant, it is less suitable for detailed study. A shorter account of its biology will be presented in a later publication.

There have been some previous accounts of the biology of *Manacus*. Chapman's pioneering study of the courtship of Gould's Manakin (*M. vitellinus*) in Panama was the first detailed study of any of the Pipridae (Chapman, 1935). Although there had been some earlier accounts, it was this paper which first drew attention to the extraordinary development of courtship behavior in the family. Working on specimens sent to him by Chapman, Lowe (1942) described the musculature of the wing-feathers and other specializations responsible for the loud mechanical noises made by the males during their displays. In Trinidad, Chapman (1894) had earlier made some brief observations on the display of *M. manacus,* and subsequent writers have occasionally referred to the males' courtship gatherings. A preliminary account of the present study, dealing only with display, has already been published (Snow, 1956). Darnton (1958) has also published some observations made at a Trinidad display ground of *M. manacus*. Finally, Sick (1959) has dealt with *Manacus* among other genera in his review of displays in the Pipridae as a whole.
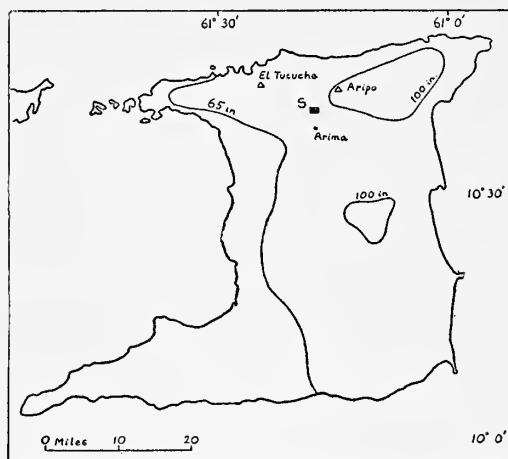
TEXT-FIG. 1. Trinidad, showing the study area (S) and the annual isohyets. The Northern Range extends along the whole of the northern side of the island, the two highest points being shown (Aripo and El Tucuche).

It may be noted that, although *M. manacus* and *M. vitellinus* have usually been treated as separate species, there are no important differences in behavior between them (Appendix 1) and morphologically they differ only slightly, *M. vitellinus* having the plumage suffused with orange-yellow which is lacking in *M. manacus*. They would thus reasonably be considered as conspecific, but for evidence that they are sympatric in Colombia (de Schauensee, 1950).

The present study is based on observations continued over 4½ years. Display was watched, and filmed, from hides at display grounds, the most complete observations being made at one display ground that was visited regularly over the whole period and weekly, except for a few gaps, from June, 1958, to September, 1961. Trapping was an important part of the work; a total of 271 individuals were caught in mist-nets in the study area, many of them repeatedly. Some 150 more were trapped in other parts of Trinidad, mainly in connection with the work of the Trinidad Regional Virus Laboratory. Each bird trapped in the study area was given a different color combination, and many of them were seen subsequently in the field. Many of the males occupying courts at the display grounds under observation were eventually color-ringed. Trapped birds were also examined for moult and other details of plumage, and were weighed. Breeding was studied by systematically searching for nests along certain stretches of forest stream, and recording their fate. Searching was continued in all months of the year, not only at seasons when manakins were known to be nesting. Twenty-eight birds were ringed as nestlings.

Some observations on behavior at the nest were made from a hide. Food was studied by direct observation of birds feeding, and by collecting the regurgitated remains of food from display grounds and from below nests.

Throughout the work, attention was directed to certain problems of general biological interest concerning the ecology of birds in tropical forest. These include: numbers, reproductive rate and the control of the population; the food supply throughout the year; the breeding season and the factors controlling it; the function of communal displays.

THE ENVIRONMENT

The lower part of the Arima Valley at 400-1,800 feet above sea level, the site of the study area (Text-fig. 3), has a natural vegetation transitional between lower montane rain forest and lowland seasonal forest (Beard, 1946). As most of the area is government forest, the greater part of this natural vegetation remains little altered except for a limited amount of lum-

TEXT-FIG. 2. Male Black and White Manakin; resting posture.
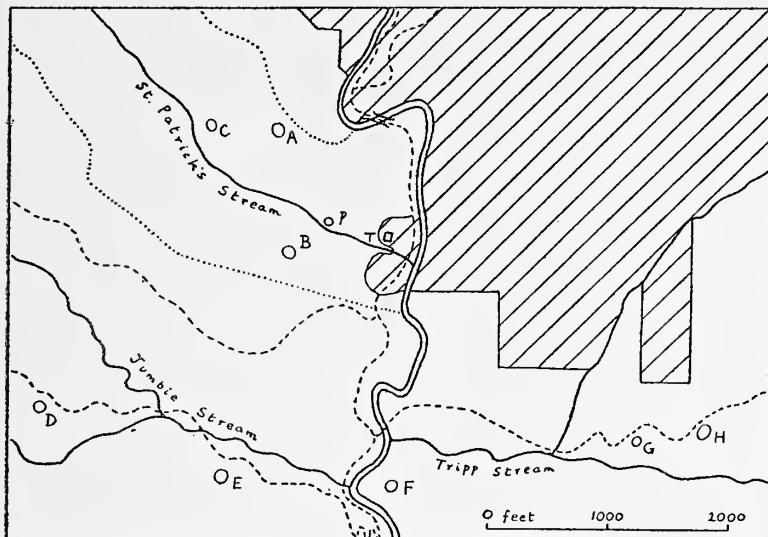
TEXT.-FIG. 3. The study area. Manakin display grounds are shown as circles and are lettered. Dotted line: boundary between St. Patrick's Estate and Government Forest. Broken lines: pathways and roads. Hatched area: unforested country.

bering, which has reduced the number of large trees of the economically important species (especially *Cordia alliodora, Cedrela mexicana* and *Carapa guianensis*). The forest is rich in tree species, many of which bear berries of suitable size for manakins to eat. The country is hilly and steep, the underlying rocks being rather soft schists.

The main Arima River flows with a gently winding course down the valley and is joined by numerous steep-sided tributaries, which in turn are joined by numerous deep side-gullies. The whole area is thus divided and subdivided into numerous ridges. The main river and the larger side-streams have water all the year round, while the gullies fill up only after heavy rain. Along the side-streams and in the gullies the dampest conditions are found; the vegetation includes tree-ferns and many smaller ferns, *Carludovica, Cyclanthus bipartitus* and species of *Heliconia.* At the other extreme, up on the well-drained ridges there is a thinner forest of trees tolerant of desiccation, among which the Yellow Poui (*Tabebuia serratifolia*) is prominent during the dry season, when it loses its leaves and produces its yellow blossoms in two or three bursts of flowering. In the dry season there is a marked contrast between the ridges, where the forest includes an important deciduous element, and the lusher vegetation along the stream bottoms.

The main road up the valley follows the river. As a consequence, the forest along the river has been much opened up and the natural vegetation modified. In particular there are great clumps of an introduced bamboo.

St. Patrick's Estate, where the two main display grounds that were studied were situated and all the trapping was carried out, is an area of secondary forest adjoining the government forest. Some large trees remain, but mostly the trees are in various stages of growth, up to a height of about 60 feet. This secondary forest is even richer in berry-bearing trees and shrubs than the primary forest. Melastomaceae are especially abundant, being represented by twelve common tree species and several shrubs. Among the lower-story trees and shrubs, in both primary and secondary forest, the berry-bearing Rubiaceae are important and are represented by many species.

Along the Northern Range the rainfall increases steadily from west to east. Port-of-Spain, at the foot of the hills at the western end, has an average annual precipitation of 55 inches, while at the eastern end the average is well over 100 inches (Text-fig. 1). The Arima Valley, half way along, has an intermediate rainfall, but closer to that of the eastern end than to the western. The average precipitation at Verdant Vale Estate, adjoining St. Patrick's, for the six years 1935-40 was 108.1 inches. The four years 1957-1960 were considerably drier, the average being only 89 inches (Text-fig. 4). Probably a long-term average would be around 100 inches at an altitude of 500 feet above sea level.

There is one main dry and one main wet season. The dry season begins in January and ends variably, usually in May. The wet season lasts for the rest of the year, but is usually broken by a spell of dry weather in September or October (the "petit carême"). Monthly totals of only one or two inches, sometimes less, are recorded in February and March; in the wet season totals of 15 inches or more are common. There is, how-
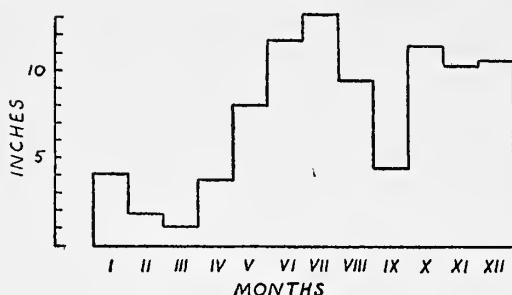
TEXT-FIG. 4. Mean monthly rainfall, 1957-1960.

ever, considerable variation in the rainfall from year to year, especially in the length and severity of the dry season. At all times of the year there is much sunshine.

Shade temperatures rarely rise above 88° F. and on wet and cloudy days they remain in the seventies. Nightly minima are usually between 65° and 75°, falling a few degrees lower on the coldest nights of the months December-March. Mean temperatures rise steadily from December to May, remain steady from May to September, then fall more rapidly from October to December (Text-fig. 5). Relative humidity is very high at nights, being always close to saturation; the day minimum varies much with location, season and weather. In two years' records an absolute minimum of 43% was recorded in March at Simla, half a mile from the study area (Beebe, 1952).
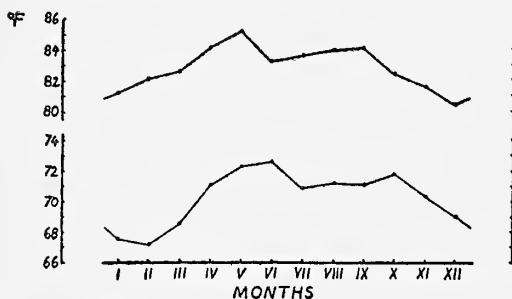
TEXT-FIG. 5. Mean monthly temperatures. St. Patrick's Estate. Upper line: mean daily maxima. Lower line: mean daily minima.

The seasons affect the appearance of the forest strikingly. Most of the trees have well-defined flowering and fruiting seasons, and all the trees of any one species are usually well synchronized. Thus when the Yellow Poui flowers, towards the end of the dry season, the forest for a few days is dotted with patches of brilliant yellow. A little later another common tree, the White Olivier (*Terminalia obovata*), loses its leaves and comes into flower, and pale yellow

patches appear all over the forest. In general, there is most flowering and most loss of leaf during the dry season, and most renewal of leaf during the wet season. In prolonged dry spells, especially towards the end of the dry season, the ground becomes parched and hard, the dead leaves on the forest floor crackle underfoot, and the leaves of the shrubs and smaller trees begin to wilt. The first heavy rain after such spells has a greatly stimulating effect on all plant and animal life, and makes the sharpest seasonal change of the whole year.

DISTRIBUTION, NUMBERS AND GENERAL ECOLOGY

No detailed survey was made of the distribution of the Black and White Manakin in Trinidad, but visits to many parts of the island showed that it occurs generally in all kinds of forest, primary and secondary, from sea level to about 2,000 feet, except for the dry forests at the western end of the Northern Range to the west of El Tucuche (Text-fig. 1). It is especially abundant in the forests of the central and eastern parts of the Northern Range, at moderate altitudes, and in the adjacent low-lying forests. This is the sector of highest rainfall, up to 100 inches or more. Above 2,000 feet, where the rainfall is considerably higher and the forest changes to the montane type, the Black and White Manakin becomes rather rare. The two highest display grounds found were on Aripo at about 2,000 feet and on El Tucuche at about 2,200 feet. Very few birds were seen on walks through the mountain forests above 2,000 feet.

Where manakins are common, display grounds are scattered at intervals through the forest. In the hilly country of the Northern Range they are mainly situated on ridges, either on the crest or a little way down one of the sides. Those in the study area (Text-fig. 3) were situated on minor side-ridges not more than two or three hundred feet above a stream bed. In low-lying country, however, display grounds are common in perfectly level forest. The preference for a situation on a ridge, where it is available, may be due to the commanding position of such a display ground over the streams below, along which the females prefer to nest.

More critical than the position of the display ground with respect to ridge or stream bed is the structure of its lower vegetation. The Black and White Manakin depends for its display on small upright saplings up to about 20 mm. in diameter. As will be seen later, two or more of these must be available within a few feet of each other to allow a bird to display fully. Further, a communal display ground cannot be established

unless there are many such groups of saplings within a few yards of each other.

The same display grounds seem to be used as long as the vegetation remains unchanged. All those that were under observation persisted for up to 4½ years, and local information indicated that they were already old. During a visit to Panama in 1958 the display ground of *M. vitellinus* studied by Chapman in 1932 was found to be active exactly in the position which he described.

In the course of the 4½ years' observations at the main display ground that was studied, the same individual saplings continued to be used, and though they were not measured when observations began they showed no apparent growth. In this, as in other respects, the tropical forest is an extremely constant, unchanging habitat. Only a few courts were abandoned, due to the fall of a mass of vines or a small tree, and some new ones were cleared, but these new ones were mainly peripheral and they did not all last long. The central nucleus of courts remained almost the same.

Text-figure 3 shows the distribution of display grounds in the area of forest, comprising some 450 acres, that was most thoroughly covered. It is unlikely that any large display grounds were not found, but small, intermittently-used display grounds (the "practice display grounds," p. 80) may easily have been missed. From the number of courts at these main display grounds it is possible to assess the number of adults in the area.

There were approximately 205 courts at the seven main display grounds known in the area. At the display ground studied in most detail (A in Text-fig. 3) it was found that in addition to the established adult males there were about a quarter as many unestablished adults. Thus 205 courts probably corresponds to some 250 adult males. Trapping showed almost exact equality between the sexes (p. 97). Thus there were probably about 500 adult birds in the 450 acres of forest.

There was no evidence for any considerable change in numbers in the course of the study. The main display ground under observation usually had from 24 to 28 active courts over the four years, and another that was observed less closely (B in Text-fig. 3) had from 30 to 33 over three years.

Although individuals are in general sedentary, there was nevertheless too much local movement for the trapping figures to be used for an independent assessment of the population. Especially during the moult there must be some individual wandering, as the proportion of birds

ringed then but never retrapped nor seen again was higher than at other seasons (47% for the months of moult, July-October, compared with 19% for the other months). For feeding, too, birds may move several hundred yards. Two males trapped at the main trapping place (T in Text-fig. 3), one of them as a juvenile, were later found established at display ground E, nearly half a mile away, and three females were found nesting about half a mile from where they were trapped. All these were probably feeding at the time that they were trapped. None was found at any greater distance from the trapping place.

In the breeding season, which lasts for several months, males and females are differently distributed in the forest for the greater part of the day. The males keep to their display grounds, up on the ridges, while the females hold small territories along the streams and gullies by which they mostly nest. The sexes meet when feeding and bathing, and also, for short periods, at the display grounds.

When feeding and bathing, males from the two display grounds A and B kept mainly to separate areas (Text-fig. 6). Thus at the main trapping place (T) many males from display ground B were trapped while feeding, most of them repeatedly, but only one male from display ground A was ever trapped there, once only. No males from display ground A were ever seen at the two bathing places nearest to T, but males from display ground B were seen bathing at them 13 times. At the bathing place nearest display ground A, on the other hand, there were 13 records of males from A bathing, and only 8 of males from display ground B.

Though no figures are available for comparison, there is little doubt that the density of the manakin population in the forests of the Arima Valley, and probably over much of Trinidad, is unusually high. *Manacus* was found to be much more sparsely distributed in various forest habitats in British Guiana, Surinam and Panama, and the published accounts from other areas are in agreement. Two factors are probably responsible for the high Trinidad population. First, the forest in Trinidad is much broken up, and there is a high proportion of second growth. Clearings, paths and roads are numerous. Where lumbering is carried out, the trees that are removed are mostly species whose fruits are unsuitable for manakins to eat (especially *Cordia alliodora, Cedrela mexicana, Carapa guianensis, Sterculia caribaea* and *Mora excelsa*). Many of the manakins' main food trees are characteristic of secondary forest and of road-edges, being relatively rare in untouched forest; this is particularly true of the most important family of
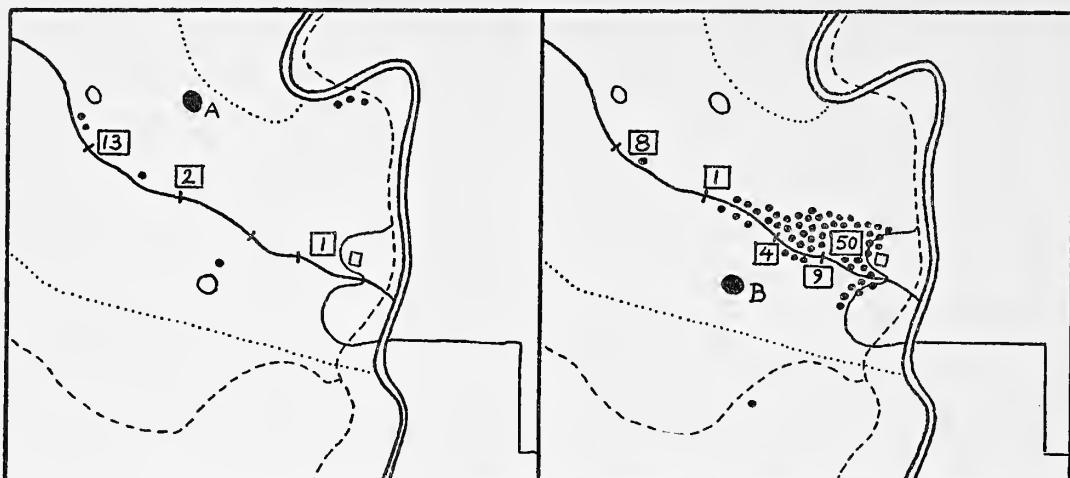
TEXT-FIG. 6. Foraging and bathing ranges of 9 males from display ground A (left) and 13 males from display ground B (right). Figures in squares: numbers of observations at bathing and trapping places. Dots: sight records of feeding birds.

all, the Melastomaceae, which flourish in second growth in areas of high rainfall and reach a great abundance in the wetter parts of Trinidad. Thus a moderate amount of clearing and lumbering benefits the manakin population. Secondly, with a reduced avifauna, compared with neighboring parts of Venezuela, Trinidad shows to some extent the phenomenon characteristic of islands: few species, but large populations of those species that are present. This must be attributed to reduced competition from other species, but the way in which this reduction of competition operates is far from clear.

DISPLAY

First Impression of a Display Ground

It is difficult to describe the activities at a display ground of Black and White Manakins in terms suitable for a scientific journal and at the same time give any adequate impression of the total effect of the bizarre postures and movements, the sharp snaps and cracks, and the extraordinary vivacity of the whole performance. Yet undoubtedly this combined effect is of paramount importance, for communal display would not have evolved if the effect of a group of males displaying at close quarters had not, for the female manakin, greater attractive power than that of a single male displaying by itself.

The first impression is bewildering. Spaced only a few feet apart (if the courts are well concentrated), a group of small black and white birds are seen leaping about and performing other evolutions with extraordinary rapidity, within a few inches of the ground. Accompanying these movements, some of which are too rapid to follow in detail by eye, are a variety of sharp cracks, like percussion caps exploding, rolling snaps, and whirring and grunting noises, as well as a chorus of excited high-pitched calls.

Closer inspection shows that each bird is performing on and around a small area of bare soil and rootlets, which shows up plainly against the surrounding leaf litter, and that two or three saplings around the edges of each cleared area are the chief perches of the displaying birds. More prolonged observation shows that the birds' bewildering evolutions can be resolved into a number of highly stereotyped movements. Surprisingly, the whole performance may be taking place, and may continue to do so, without the presence of a single female. But if a female does appear, the intensity of display will at once increase.

Anatomical Specializations of the Male and the Mechanical Sounds

Lowe (1942) made a detailed examination of the plumage and musculature of *Manacus vitellinus* and described the structures responsible for its specialized displays. In its morphology *M. manacus* seems to be identical with *M. vitellinus,* and its displays are almost identical. Here only a short summary will be given of the anatomical findings. It is still not certain how all the mechanical sounds are made. As Sick (1959) remarks, full elucidation will depend on experiments on birds displaying in aviaries.

Both the primaries and secondaries are modified in the male. The four outer primaries are very narrow and stiff, the outer webs especially

being extremely narrow. Due to this, the male makes a grasshopper-like whirring in level flight which is automatic and not a part of any display. Females and young males, which have unspecialized primaries, make only a low whirr when they fly, and moulting males that have lost some of their outer primaries also fly comparatively silently. However, the attenuated outer primaries are probably also responsible for the sound made during "fanning," a display to be described later.

The secondaries are more highly modified. Their shafts are unusually thick, and the outer webs very stiff. In addition, the ends of the quills are not attached to the ulna but pass dorsally to it and are loosely attached to a tendon that runs along the dorsal side of the radius. The muscle slips attached to the bases of the secondaries are very highly developed. The secondaries thus have great mobility.

These modifications of the secondaries are undoubtedly responsible for the two loudest mechanical noises made in display, the single "snap" and the "rolled snap." A single "snap" is made each time the displaying bird jumps from one perch to another; it is also made, much less often, by perched birds. In either case the wing movement is much too rapid for the details to be seen. The "rolled snap" is also made when perched or just before taking off for a leap or short flight. As it is made the wings can momentarily be seen raised above the back and vibrating rapidly. Both in the single and the rolled snap the actual sound is probably made by the stiff outer vanes of the secondaries brushing against one another rapidly as the wing is opened and closed, partly through the action of their muscles and partly due to the nature of their attachment along the radius.

More general muscular modifications are also important for the display. In particular there is a great development of the pectoral musculature (responsible for the very rapid wing-actions needed for "snapping"), the thigh musculature (responsible for the powerful leaps from perch to perch), and the muscles moving the tail (connected with the rapid turning about in mid-air during jumps between perches).

The appearance of the head is much altered during display. Most striking are the elongated feathers of the throat, which are puffed out to form a white "beard" protruding beyond the tip of the beak. Connected with this, Lowe reported a noticeable development of the unstriated muscles activating these feathers, and also of the muscles of the hyoid apparatus. The neck feathers, and the feathers of the sides of the head, are also greatly puffed out, so that the black cap

is transformed from a broad oval to a narrow slip of black tapering to a point at the posterior end. Seen from the front the bird appears all white with a small black lozenge in the middle. Probably the neck feathers too are provided with a specialized musculature.

VOICE

Black and White Manakins utter a variety of rather simple, mainly monosyllabic, calls. Undoubtedly the very loud mechanical snaps have functionally replaced the loud and more complex calls of some other manakins and the related Cotingidae. Nevertheless some of the calls are quite loud, and they make up an important part of the total volume of sound heard at an active display ground.

The only call of the adult that is unconnected with display and uttered by both sexes is a rather plaintive monosyllabic "peerr," slightly trilled at the end. It is uttered by alarmed birds, such as females whose nests have been approached or males disturbed at a display ground, by solitary birds away from display grounds or nests, and by males sitting quietly at the display ground between bouts of display. In aggressive encounters between males, it is uttered by the subordinate bird.

As the excitement of a male mounts, his calls change from the unexcited "peerr" to a louder, higher-pitched and untrilled "chwee." This is the dominant vocal sound made during the outbursts of calling and snapping which greet the arrival of a female at a display ground.

The "peerr" call has other variants that sound like "pee-you" or "pee-yuk," being more disyllabic, with the trilled ending modified into a more distinct separate note. Chapman described these as "notes of awareness, address and response, or of inquiry or protest"; certainly they have a varied social significance that cannot be simply defined. They are uttered by males at display grounds in a variety of circumstances, but not in the immediate presence of a female.

A quite distinct call, a disyllabic "chee-poo," typically marks the beginning of a bout of display. Frequently it follows immediately after a rolled snap. It is not uttered in other circumstances.

Juvenile males, when displaying, sometimes utter a rather soft, plaintive "pu." In *M. vitellinus* this call is associated with a stereotyped display (Appendix 1), but in *M. manacus* it seems almost to be obsolescent, since it was rarely heard, and then only from juveniles when engaged in uncoordinated display with other young birds.

The begging calls of young birds, in the nest

and when being fed after leaving the nest, are described elsewhere (p. 89 and 90).

THE COURT

The general character of the display ground has already been described, and the constancy of the courts from year to year mentioned. The spacing of the courts at different display grounds is variable. If there are sufficient suitable saplings, most courts may be within a few feet of each other and clusters of two or three may be in contact with each other. If groups of suitable saplings are fewer, courts may be many yards apart. At the largest display ground seen in Trinidad (H in Text-fig. 3) there were some 70 courts, many of them almost touching each other, within an area of about 20 by 10 yards. More commonly courts are on average from one to five yards apart. The display grounds of *M. vitellinus* studied by Chapman in Panama were far more scattered, and also very small, with not more than five courts spaced as much as 200 feet apart. This situation is probably unusual; at another display ground in Panama visited in 1958, the spacing of the courts was the same as in Trinidad.

The size of a court is also variable. Most are roughly oval and measure about 3 by 2 feet. From this area all dead leaves are carried away and most of the rootlets are stripped white by the owner's continual picking at the bark. All that remains is bare earth, rootlets and such sticks as are too large for the bird to carry away.

One of the upright saplings growing round the court is more important than the others, in that some of the main displays, and mating itself, take place on it. This "main upright," as it will be called, must be fairly straight and smooth; those that were measured were not less than 6 mm. or more than 20 mm. in diameter near the ground. Its bark is usually worn smooth by the continual rubbing of the bird's feet, and below it the ground is kept especially well cleared.

The birds clear their courts at intervals throughout the day, usually during bouts of display. Typically, the bird jumps down onto the ground beside the object, usually a leaf, which is littering the court, picks it up and flies to a perch a few feet away, dropping it as it lands. Or it may lean down from a low perch at the base of a sapling, pick up an object and fly away with it. Less often, a bird flies down and without alighting, or alighting for only a fraction of a second, picks up a leaf and flies off with it, the whole movement being so rapid that it is impossible to see in detail.

THE ELEMENTS OF THE DISPLAY

The different displays were seen very many times and were recorded on 16 mm. movie film, usually at 24 frames per second (the light at the display grounds was not good enough for exposures shorter than 1/50 second). This account differs to some extent from previous accounts of the display of *M. manacus*. Previous observers have not seen all the displays, and their accounts of some that they have seen have been inaccurate. This is not surprising; conditions of observation are often not easy, and in any case very fast display movements need to be seen many times, and over a long period, before their exact nature becomes clear.

There are also some differences between this account and Chapman's account of the display of *M. vitellinus*. Some of these seem to represent real differences between the behavior of the two species; they are dealt with fully in Appendix 1.

The "snap-jump"

This is the most frequently used of the display movements. Typically, the bird perches in a horizontal position across one of the upright saplings round its court, with its head thrust forward and beard extended, then suddenly with a loud snap leaps to another perch, reversing its position as it reaches the other perch so that it lands facing the way it came from (Text-fig. 7). The complete leap from one perch to an-

| 1 | 2 | 3 | 4 |
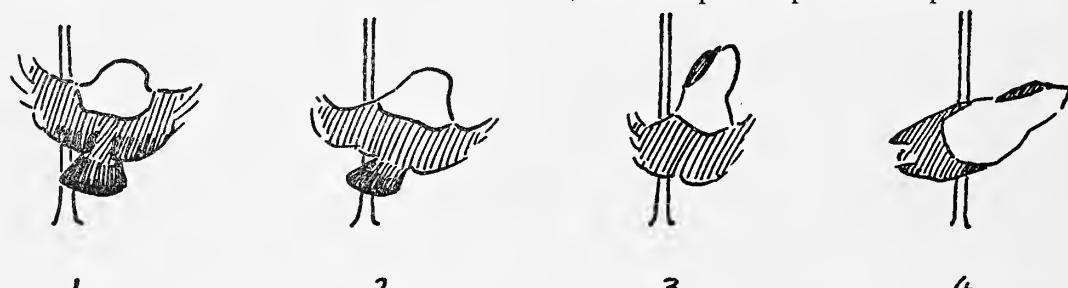
TEXT-FIG. 7. The "snap-jump": a male turning in the air and landing after the jump. The bird approaches the perch in an upright position (1), tucks tail under, at the same time turning head and neck (2 and 3), and lands facing the way it came from (4). (Drawn from movie film.)

other usually lasts from one-sixth to one-quarter of a second, depending on the distance between the two perches. During the jump, the whirring noise made during normal flight is not heard.

Many snap-jumps may be repeated in quick succession, so that the bird crosses and recrosses its court with great rapidity. When more than two perches are available, there is a tendency for the sequence of snap-jumps to follow a fixed pattern from one perch to another.

Because the snap and the jump are simultaneous, it would seem that the snap depends on the wing-movements involved in the leap. Very occasionally, however, a bird makes a snap and remains perched, but such snaps are less loud than those accompanying a jump.

The "rolled snap"

The bird leans forward on its perch, raises its wings above the back, and with a vibrating movement that is almost too rapid to see emits a loud rolling snap, like a succession of single snaps run together. It frequently takes flight immediately afterwards, or if it does not fly utters a call, "chee-poo," indicative of mounting excitement. The rolled snap typically introduces a bout of display after a period of inactivity.

The "grunt-jump"

This follows after a sequence of snap-jumps between the saplings round the court. The bird jumps or flies to the "main upright," landing transversely on it within a few inches of the ground, then with beard extended, body tensed and even quivering slightly, as if bracing itself for the effort, it leaps down to the ground, turning in the air as it does so, lands momentarily on its feet facing the perch, and leaps back to a higher position on the same perch (Text-fig. 8). As it leaves the ground it emits a curious sound between a grunt and a whirr. The whole sequence, from leaving the perch to landing on it
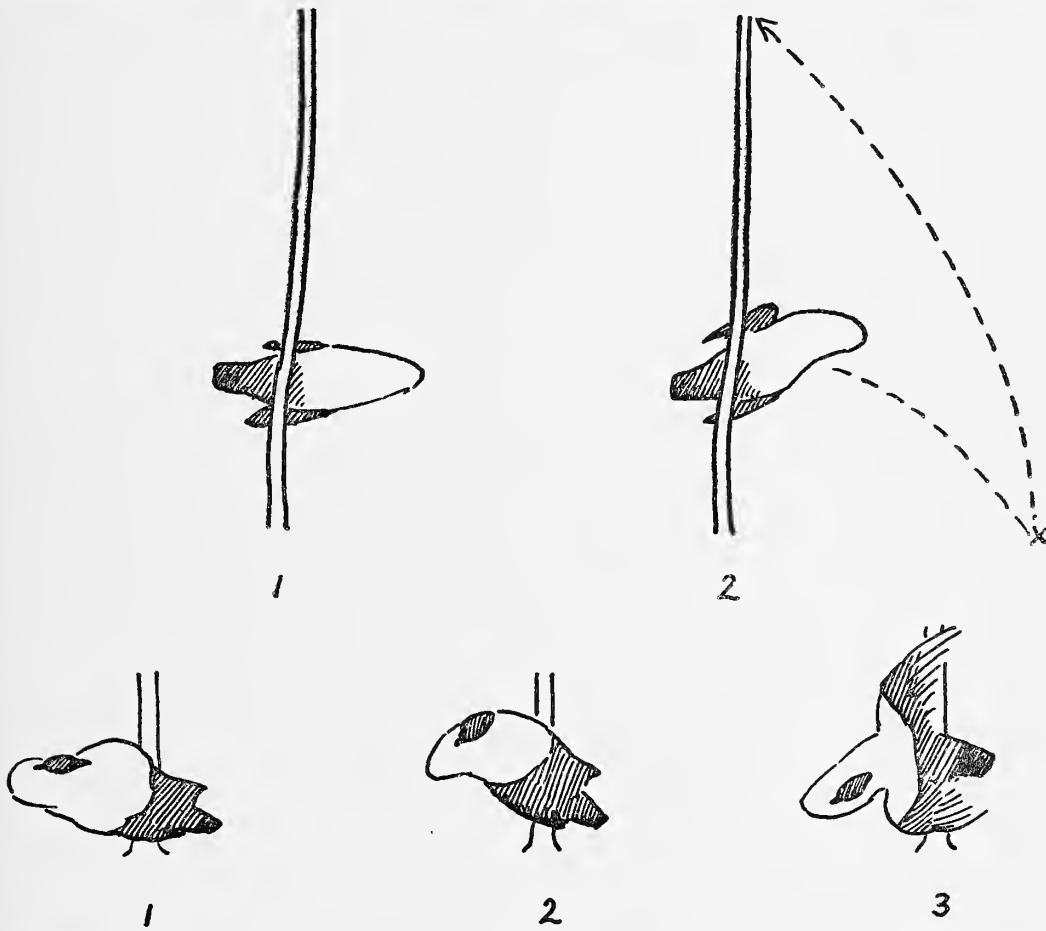
TEXT-FIG. 8. The beginning of the "grunt-jump," from two viewpoints, showing the bird's trajectory (right, upper). Just before jumping, the bird raises its head and neck and half-opens its wings. (Drawn from movie film.)

again higher up, is extremely rapid and difficult to follow by eye; it lasts just over one-third of a second.

The same grunting sound is occasionally made by perched birds, and is accompanied by a sudden humping up of the back, the head being held forward and rather low. At the same time the wings are moved, but too rapidly for the details to be seen. The grunting sound thus made is a little lower-toned, lasts longer and is more vibrant than that made on an upward jump. A sound approaching the grunt is also made when a bird rapidly flies upward from the ground to a perch, or from one perch to another. Thus the sound is certainly mechanical in origin but it is not clear how it is made.

The "slide down the pole"

Immediately after landing on the main upright, after the "grunt-jump," the bird may move down the perch for several inches in a head-downward position, with the wings beating, moving with such short steps that it appears to slide. As it approaches the bottom of the sapling it turns to a more horizontal position (Text-fig. 9). This display is comparatively infrequent.

The "grunt-jump" followed by the "slide down the pole" represent the culminating phase of the courtship display in that they immediately precede copulation, as described later (p. 77). The male "slides down the pole" on to the back of the female, who perches below him on the sapling.

"Fanning"

This is a very distinct display. The male leans forward on his perch, holding his head low, with the neck retracted and the beak pointing slightly upwards, and sways his body from side to side. At the same time he holds his wings out from the body and beats them at the rate of five times per second, raising and depressing the tail and the whole hind end of the body synchronously. The beating of the wings makes a low-frequency whirring sound, easily distinguishable from the flight whirr. Apparently due to the retraction of the head between the "shoulders," as the wings are raised the feathers of the hind-neck are pushed forwards and upwards so that they stick out as two flickering white puffs behind the bird's head at either side (Text-fig. 10). This display is most often directed at a female which has approached a male's court. Several seconds of fanning, during which the male may repeatedly shift his position so as to present himself to the female, are usually followed by his flying to the court and executing a series of rapid snap-jumps. The display is also occasionally performed when no female is present.

The upright posture

Displaying birds sometimes assume an upright
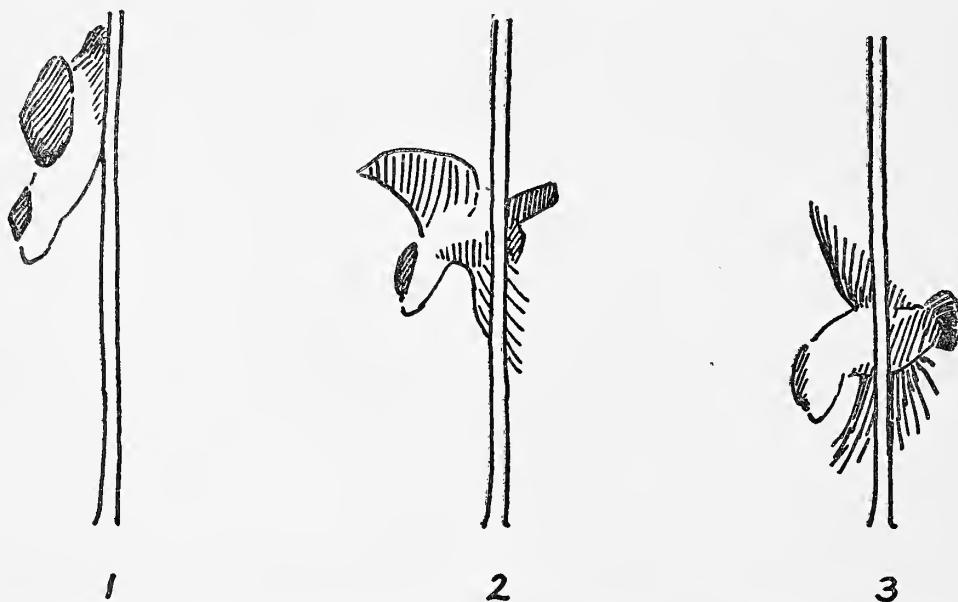
TEXT-FIG. 9. The "slide down the pole." (1) the beginning of the slide, just after landing from the "grunt-jump." (2) half way down. (3) near the end of the slide, the body becoming more horizontal and the tail fanned. (Drawn from movie film; no attempt has been made to show the feet, which move too fast to appear on the film.)
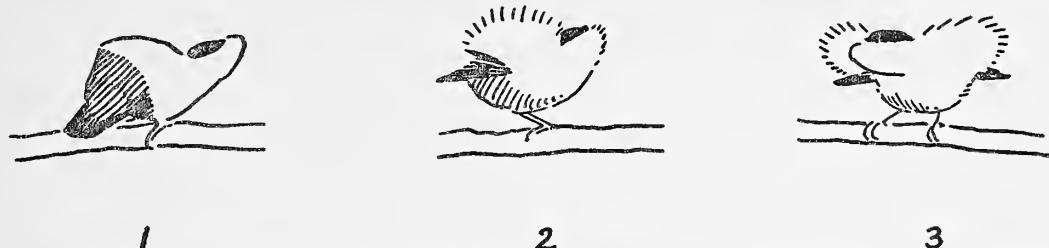
TEXT-FIG. 10. "Fanning." Left, (1) and (2): wings closed and wings raised. Right (3): wings raised, seen from the front. (Drawn from movie film.)

posture when perched, with the head pointing upwards and beard extended. This posture does not seem to play an integral part in any of the main display movements described above, though it sometimes follows a bout of snap-jumps. The posture may be held for several seconds.

Aggressive displays between males

When two males are perched close together, the dominant one may extend his beard, turn about frequently on his perch, give little jumps along the perch, hold his head low and turn it from side to side, or raise and vibrate his wings, all these being incomplete forms of normal sexual displays. Sometimes he may fan his tail and turn it towards the other bird. The subordinate bird sits quietly, with throat and body plumage sleeked; when threatened he may flick his wings and suddenly fan and close his tail, probably flight-intention movements. Aggressive behavior between males may culminate in prolonged flight chases round and round the display ground and in fights on the ground.

THE DAILY RHYTHM OF DISPLAY

Apart from the weeks when he is moulting, the adult male manakin is at all times closely attached to the display ground. Almost as soon as it is light enough to see, the first males appear at their courts. Display soon begins and reaches a peak, then after an hour falls off to a low point between 0900 and 1100 hours. In late morning the intensity of display increases again and reaches a second peak around 1400; it then falls off again gradually and by 1700 has practically ceased. The males gradually move away, a few late ones remaining until about 1800. The precise times of the beginning and end of display vary somewhat, depending on the times of sunrise and sunset and on the variations in light intensity due to weather and the forest canopy.

Text-figure 11 shows the results of a continuous watch on a single ringed male throughout the daylight hours of January 27, 1960, a day of moderately intense display. Between 0625, when he arrived, and 1747, when he finally left, he was present and under observation for 90% of the time. He was probably present for somewhat longer than this, as at times he perched a few yards away from his court in a place where he could not easily be seen, and thus he was recorded as absent for a few short periods when he was almost certainly present. His 24 recorded absences nearly all lasted less than 5 minutes. During one of the longest absences, of 6 minutes from 1659 to 1705, he certainly bathed, as he returned looking dishevelled and preened vigorously (and this is the time when observations by forest streams showed that bathing activity is at its height). There was no reason to suppose that this bird's activity on this day was in any way unusual. Less complete observations on many other birds showed a similar degree of attachment to the display ground throughout the day.

Females visit the males at their courts mainly during the two periods of intense display (0630-0800 and 1330-1500). Intensity of display by the males and the presence of the females are of course interrelated, in so far as the presence of a female stimulates the males, and intense display by the males attracts the females. But apart from this, the males' daily cycle of display is to a great extent independent of the females, as it is equally marked at seasons when the females are visiting them hardly or not at all. On the day when a continuous watch was kept, only one visit by a female was recorded in the afternoon. This was unusual; typically as many females are seen visiting the males in the afternoon as in the early morning period.

Text-figure 11 shows that the male under observation left the display ground, presumably to feed, mainly at times when display was slack, and that his first absence took place soon after 0800, when the early period of intense display was over. Trapping and observation away from the display grounds confirmed that these are the main feeding times. In particular, trapping at a feeding area (T in Text-fig. 3) regularly
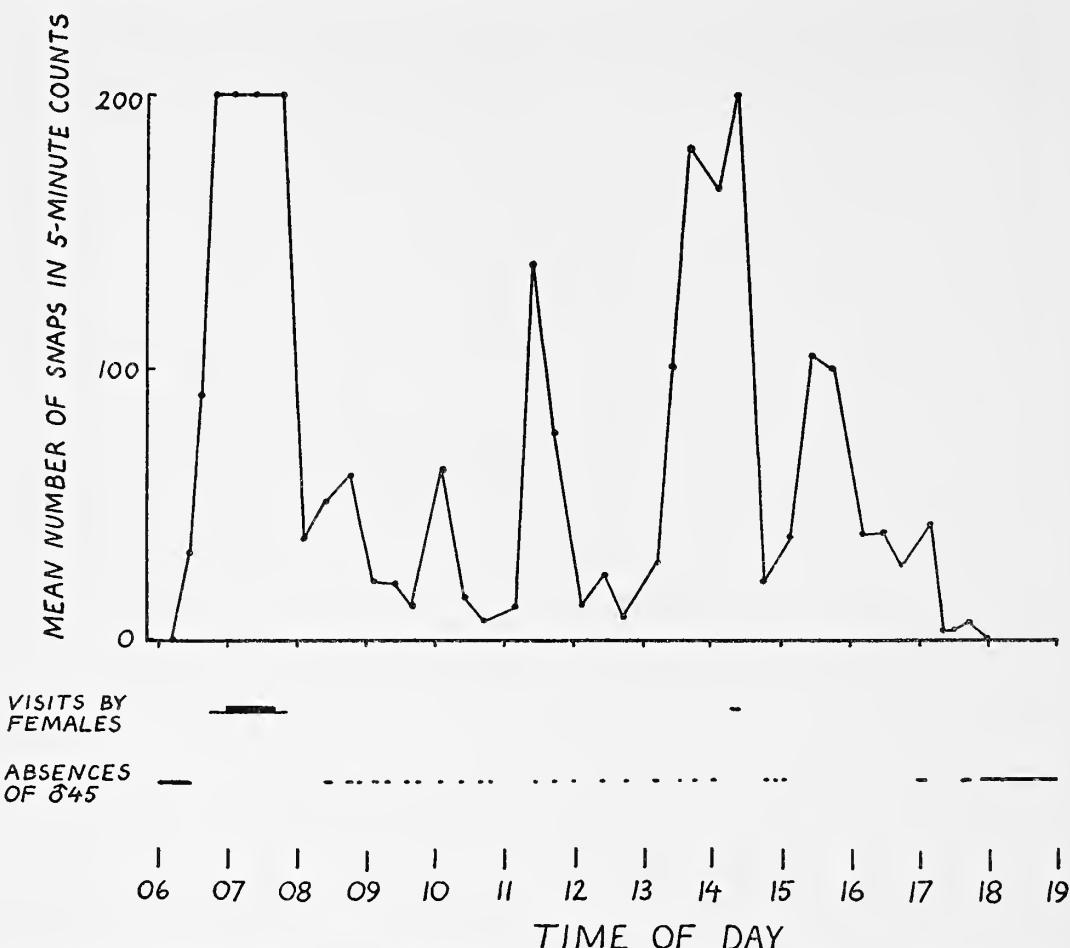
TEXT-FIG. 11. The activity at display ground A, January 27, 1960. Intensity of display measured by number of snaps in 5-minute periods (snaps in excess of 200 omitted). Female visits: thin line, one female present; thick line, several females present.

showed a period of great activity in the hour between 0800 and 0900. Text-figure 12 shows the numbers of males, known to have courts, that were trapped in this area in the different hours of the day.

It was also found that, at least occasionally, males may feed intensively in the short period between first light and their arrival at the display ground. This may depend on the availability of fruiting trees in the forest canopy or in open places along the forest edge, where the light allows feeding at such an early hour.

Displays Between Male and Female

Males display vigorously and perform all the display movements described above when no female is present, as already mentioned. But the arrival of a female leads to especially intense and sustained display. Indeed the observer is usually first made aware of the presence of the cryptically colored female by the upsurge of display and calling.

Her arrival is usually greeted by an outburst of rolled snaps, as males fly to their courts to display, by an intensification of the single snaps, as males that are at their courts perform rapid snap-jumps, and by a change in the calling from an occasional "peerr" to a chorus of excited "chwee" calls. If the female approaches a male's court, he may fly to her and, landing beside her, give a prolonged display of "fanning," after which he will usually fly down to his court and perform a series of rapid snap-jumps.

There is always a strong tendency for the males to fly towards the female as well as to go to their courts and display. Sometimes several males will fly towards her while she is still at the edge of the display ground, and though

quantitative observations on this point would be difficult and were not made, the tendency seemed to be strongest in the first weeks after the moult, and in those males that were less settled at their courts. The tendency for males to fly towards a female is also strong when, as sometimes happens, she flies in high and perches well above the courts. Several males then often fly up to her and call and snap excitedly, but in such cases the female appears unwilling to go down to the courts. Females that are ready to join the males at their courts fly in only a few feet above the ground.

Usually males do not approach a female until she is within a few yards of their court, and they then perform the fanning display at her. Fanning is a clear indication that the female is within the male's sphere of influence, even though she may still be several feet from his court. Two males were never seen fanning simultaneously at the same female.

The behavior of the females when they first arrive at the display ground is quiet and almost secretive. They flit from perch to perch, within a few feet of the ground, and show signs of initial nervousness. Early in the season, before breeding has begun, they often arrive in groups of up to five together; later they more often come singly.

Early in the season they not only arrive together but also go down to the courts in groups, and a rather confused display develops. The male displays hard, but at the same time seems somewhat "taken aback" by the number of females present. They perch on the surrounding saplings and on his court, frequently flitting from one perch to another and changing places with each other, keeping clear of the male and yet plainly attracted to his court.

But when a single female visits a male at his court a well coordinated display or dance may take place, which may culminate in copulation.

These dances become commoner as the breeding season approaches. As would be expected, all transitions may be seen between the confused situation with several females present at a court and the highly coordinated dance between the male and a single female.

A full sequence of the precopulatory display is as follows. The female approaches the court; the male flies to her and "fans" for several seconds; the male then flies down to his court and executes a rapid series of snap-jumps; the female soon follows, landing on one of the upright saplings; a mutual dance then takes place, with the male doing repeated snap-jumps across the court and the female crossing him in mid-air and landing at the place which he has just left; after a series of these jumps, the female lands on the "main upright;" the male jumps and lands below her on it, then immediately executes a "grunt-jump," going down to the ground and back up onto the main upright above the female; he then "slides down the pole" onto her as she is perched crosswise on it, and copulation takes place; during copulation the male has one foot on the perch and one on the female's back.

More often, only a part of this sequence is seen. In particular, the preliminary fanning, which serves to attract the female to the court, is usually given only to hesitant females, and such birds, when they do go down to the court, usually do no more than a few jumps with the male. On the other hand, females that are ready to copulate often fly straight to the main upright and the male at once follows with the sequence "grunt-jump"—"slide down the pole"—mounting. It was sometimes observed, and is probably usually the case, that these birds had recently visited the male and had danced with him several times.

When females first dance with a male they are nervous, and the males in their turn sometimes behave aggressively towards them. The female tends, when flying to the perch that he has just
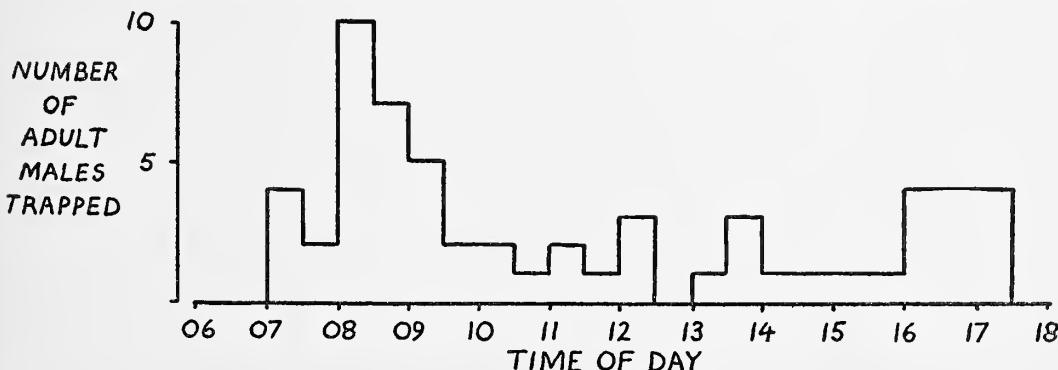
Text-fig. 12. Numbers of adult males with courts trapped at a feeding area throughout the day.

left, to keep a little higher. Thus the two birds cross in mid-air with the female a little above. This tendency to keep above the male is undoubtedly an indication that the female is not ready to mate, to do which, as described above, she must allow the male to land above her on the same upright. If the male, perched below her on the main upright, does a "grunt-jump" to land above her, the female, if not ready to mate, at once flies to another perch.

The females that visit the same display ground probably have a mutually stimulating effect upon one another. As already mentioned, they tend to come to the display ground in small groups, especially at the beginning of the season, and at all times the outburst of display that accompanies the visit of one female to the display ground must help to attract other females. As a result, there is a tendency for the nests near any one display ground to be better synchronized with each other than with nests near other display grounds (Table I).

TABLE I. SYNCHRONIZATION OF NESTINGS OF FEMALES ALONG THE SAME STRETCHES OF STREAM, 1961

	Number of nests started along different stretches of stream (see map, Text-fig. 3)		
	Tripp Stream	Arima River	St. Pat's Stream
Feb. 26-Mar. 1	3	1	—
Mar. 2-6	2	1	—
Mar. 7-11	—	—	—
Mar. 12-16	1	4	2
Mar. 17-21	1	—	1
Mar. 22-26	—	—	—
Mar. 27-31	1	—	1
Apr. 1-5	2	—	—
Apr. 6-10	3	—	2
Apr. 11-15	1	—	1
Apr. 16-20	2	2	—
Apr. 21-25	1	—	—
Apr. 26-30	—	—	—
May 1-5	—	—	1
May 6-20	—	—	—
May 21-25	—	—	1
May 26-30	—	—	1
May 31-June 4	—	—	2
June 5-9	4	—	3
June 10-14	5	—	1
June 15-19	1	4	1
June 20-24	—	1	1
June 25-29	1	—	—

Notes. A small number of nests started after the end of June are omitted.

The "Arima River" nests were all situated along the 600-foot stretch west and south of display ground F, at the lower edge of Text-fig. 3.

CHOICE OF DISPLAY PARTNER BY VISITING FEMALES

At the main display ground, 39 color-ringed females were seen visiting the courts and dancing with males, most of which were themselves color-ringed. Three of the females were seen visiting the display ground in three successive years, and eight in two successive years.

There was no evidence for any kind of pair-formation at the display ground. Without exception, all those females that were seen visiting more than once (21 out of the 39) visited and danced with more than one male. Usually in the course of a single visit females went from one male to another. They all undoubtedly went to many more males than they were seen to visit, since they are difficult to follow as they flit silently from court to court in the undergrowth.

Certain males were outstandingly successful in attracting females, especially ♂ 45, whose court was close to the hide. Twenty of the 39 color-ringed females visited him, as well as many unringed females. The large number seen visiting him was only partly due to the fact that his court was easy to observe, as only four color-ringed females were seen to visit an adjoining court, and at two other close courts, also easy to observe, only 9 and 12 were seen. In the early part of the season ♂ 45 was regularly visited by four or five females together, while the males displayed persistently but vainly at neighboring courts. Within the area under detailed observation, two other males were also very successful, but because their courts were farther from the hide and the undergrowth round one of them was rather thick, only 17 and 4 color-ringed females were identified visiting them.

There was no obvious reason for ♂ 45's success. He was an old bird, established when trapped in 1958. He was constantly at his court, but not more so than many other males, and his court was not obviously more suitable than many others. He displayed vigorously, but so did most other males, and the display movements are so stereotyped that no differences could be seen between his display and that of his neighbors. His success remained high in all three years: 7, 7 and 11 color-ringed females were seen visiting him in the years 1959-61, the higher number in 1961 being probably due to the greater number of females in the population that were ringed by then.

Copulation is seen much less frequently than the courtship dances. As mentioned above, it often takes place rather suddenly, with little preliminary display. Only for ♂ 45 was any worthwhile record obtained. He was seen copu-

lating with two different color-ringed females and 15 times with unringed females. At the least he must have copulated with three different birds in a single season, and undoubtedly with many more, since observations were usually made on only one morning a week.

RELATIONS BETWEEN MALES AND THE OWNERSHIP OF COURTS

During most of the year there is little overt aggressive behavior between the males. With the ownership of their courts uncontested, neighboring males perch and display close to each other without hostility. Nevertheless competition for courts is strong, and when one falls vacant it is usually soon taken over by another bird, either an unestablished bird or one that has been occupying a less suitable court.

Some males remained unestablished for months. Such birds often display for periods at one of the outlying courts of a display ground, but they do not occupy them permanently. They shift frequently, and when an opportunity arises move to a more central court. It is because males do not remain satisfied with outlying courts that the courts in the central nucleus of the display ground remain much the same year after year, while the number and positions of the outlying courts change.

Unestablished males sometimes hang about for days round the edges of an occupied court, coming down to it and displaying when the owner is away and vacating it as soon as he returns. There were also several cases of what appeared to be joint ownership of a single court. This situation was usually short-lived, except at one court where it continued for 7 months. The two males would sit together within a few inches of each other on the court. However, one (a ringed bird) was dominant and it alone displayed when both were present, the other bird only when it was alone, and then only hesitantly. The two birds had a strong tendency to leave the court together and return together.

In such cases, as long as one bird is clearly dominant and the other subordinate, there is no open hostility between them, aggressive behavior being limited to the posturing described above (p. 75). But it occasionally happens that an intruding male actively tries to oust the owner and does not assume a subordinate position. Then prolonged flight-chases may take place, the owner pursuing the intruder, who does not leave the display ground but flies round and round. Or the two birds may come to grips and roll together interlocked on the ground. The main display ground under observation was on such a steep slope that when this happened the two birds would roll helplessly downhill over their neighbors' courts.

During the moulting season temporary changes of ownership are frequent as old birds abandon their courts, and newcomers, in many cases young males who have completed their moult earlier (p. 85), take them over. But when the moult is over and the old birds have returned, the courts normally revert to their original ownership and the position becomes stabilized. It is then rather rare for an established bird to be ousted by another. Only one such case occurred in the part of the display ground, comprising some 16 courts, that was under the most detailed observation, and the ousting was only temporary. The aggressor, ♂ 109, though an old bird, was of unsettled habits. From March, 1959, when he was trapped, to May, 1960, he had held one court, abandoned it and disappeared for three months, and had then occupied another court. At the end of May he abandoned this court too and began to hang about round the edges of the court of ♂ 45, already mentioned as an outstandingly successful old bird who had been in possession of his court for at least two years. On May 31 these two were apparently involved in a fight, which unfortunately was not seen. ♂ 109 was seen in the afternoon at one of the bathing places, with the side of his head bloody and his plumage dishevelled. On the next morning he was in possession of ♂ 45's court and ♂ 45 was not present. But a week later ♂ 45 was back in possession. ♂ 109 was again hanging about round the edges of the court and later he shifted back to his second court, which he retained for over a year until observations ceased.

Once a male is well established at a court, his tendency to keep to it still needs constant reinforcing by the presence of his neighbors at the surrounding courts. This is particularly clearly seen in the early part of the moulting season. The display ground is then largely abandoned except for some of the later males which have not yet begun to moult. These birds move about and display freely at courts at which they have never been seen displaying before. A little later, when the young males that have completed their moult come to the display ground and try to establish themselves, they too move from court to court and seem unable to settle at one court while others remain unoccupied.

Unestablished males occasionally shift from one display ground to another. Ten color-ringed males were seen frequenting two different display grounds (A and B, and in one case A and C; Text-fig. 3). Seven were known to be young birds that had not yet settled, three of them

being still in juvenile plumage. Two others were adults, but were unestablished and had probably only recently moulted into adult plumage. The tenth was an old male (adult when ringed a little over a year earlier), which, having tried unsuccessfully for a year to establish himself at display ground A, shifted to another (C), where he acquired a court.

Though they are aggressive towards each other, males have a strong tendency to sit within a few inches of each other on neutral ground between their courts, especially between bouts of display. Sometimes, but by no means always, slight movements and postures show that one is mildly dominant to the other. The same is also seen when one male is hanging about round the edge of another bird's court; the two spend much time sitting together when display is slack. Also in the case of apparent joint ownership described above, the two males would sit for long periods close together. As a result of this tendency, at times when display is slack the owners of courts that are close together spend much more time at the display ground than the owners of the more isolated courts.

Obviously, this strong social tendency is essential to the maintenance of a communal display ground. Aggressiveness and sociability are so balanced as to result in a compact group of constantly maintained, individual territories.

Mutual stimulation is also of great importance in raising the intensity of display and so more effectively advertising the display ground. Though display is inhibited when two males are too close together through competition for the same court, in the normal situation display by the owner of one court conspicuously stimulates the neighbors to display. In the absence of females display thus tends to occur in bursts, one bird starting and setting off the others. The chorus of rolled snaps that introduces these bursts is one of the characteristic sounds of a display ground.

The Settling Down of Young Males at the Display Grounds

Juvenile males moult into adult plumage in their second summer, between June and September. Before this they are indistinguishable in color from the females, but their behavior differs and it is not difficult to tell the sex of a female-plumaged bird when it has been watched a few times in the field.

From as early as twelve weeks after leaving the nest they begin to make incipient display movements. They become highly social and move about in small groups which may be seen performing uncoordinated display, often in company with one or two males in adult plumage. Often they display well away from a display ground, but they also regularly visit the display grounds and hang about round the periphery, where they are often joined by the unestablished adult males attached to the display ground. They perform all the display movements of the adult males, but as their wing-feathers are unmodified the mechanical sounds are softer, the "snap" being reduced to a "snip." The displays are also more confused. When displaying together, they have a strong tendency to fly to a perch that another bird has just left; thus they are continually changing places. At times they utter a distinctive call heard only in this context, a plaintive "pu" (p. 71).

In the study area there was a small tract of secondary forest where juvenile males and unestablished older males displayed so regularly that several small courts were created, 10 to 20 yards apart, some of which remained more or less clear for months, while one remained for nearly three years. Altogether, 18 different color-ringed males were seen displaying at these courts, as well as many unringed birds. Nearly all were juveniles or birds known to have only recently moulted into adult plumage; the two exceptions were adult males from a neighboring display ground. In addition, four females were seen displaying with the males; three of these were known to have nesting territories very close at hand. The use of this "practice display ground," as it may be called, became a tradition in the local population. During the period of observation none of the courts was ever occupied continuously for any length of time by a single male. No other practice display grounds were found, but their intermittent use would make them difficult to find except in areas which are under regular observation.

While moulting into adult plumage the young males stay away from the display grounds and, like the moulting adults, become inconspicuous. When their adult plumage is complete they reappear and become bolder, temporarily occupying courts vacated by moulting adults. But they cannot maintain their ownership when the adults return, and there begins a usually prolonged unsettled period, during which they try to establish themselves at a court.

Fairly complete information was obtained on 11 color-ringed birds during this period, and less complete information on several others. All these were watched first as juveniles, and then for at least a year after their moult into adult plumage. All moulted into adult plumage in the months June-October.

There was a strong tendency for all these

birds to occupy courts temporarily and shift for no obvious reason, and it was never possible to be sure if a court, once occupied, was going to prove permanent or not. Of the 11 birds, one was established by the following April, one by the following June, and one not until the second February after its moult. Another held a court in the February following its moult, but in December moved to another court, which at the time observations ceased appeared to be permanent. Another was definitely not established in the second February after its moult but established itself two months later. Thus these five birds established themselves approximately 8, 10, 16, 18 and 20 months after their moult to adult plumage. The remaining six birds were less successful; all were still unestablished after periods ranging from 12 to 24 months.

The history of ♂ 114, the bird that established itself in the second February after its moult, was known in some detail. It hatched in August and left the nest on September 2, 1958. It was retrapped in April, 1959, and color rings were added to the numbered ring that it had been given as a nestling. It was subsequently seen three times in June, once displaying at the practice display ground with another probably juvenile male, and once at one of the outlying courts of display ground A with several other probably juvenile males. It was last seen in juvenile plumage on June 24, being seen again in full adult plumage on October 31, when it was again displaying at the practice display ground. From November onwards, though it was seen displaying five more times at the practice display

ground, it frequented display ground A more and more. Usually it appeared nervous and hung about round a group of central courts. In March, 1960, it tried unsuccessfully to clear a court in a rather unsuitable, but central, place in the display ground. From the end of June to mid-October it was not seen and was undoubtedly moulting. It reappeared on October 18 and from then onwards was constantly present, sometimes displaying at unoccupied courts and sometimes hanging about. In February, 1961, at 2½ years old, and 1½ years after moulting into adult plumage, it began to clear a new court a few yards from the central nucleus of courts, and though the site was not very suitable it successfully cleared it and held it until the second week of September, when it again disappeared for the moult.

THE ANNUAL CYCLE

The Annual Cycle of Display

As already mentioned, except when they are moulting the adult males are normally present at the display ground throughout the year. From the beginning of August, 1958, to the end of July, 1959, an early-morning watch was made each week at the main display ground under observation, and a quantitative record was kept of the intensity of display by counting the snaps accompanying each display jump. Text-figure 13 shows the intensity of display as thus recorded through a complete year, based on the average number of snaps per 5-minute period recorded in the hour of most intense display. The figure also shows the numbers of females recorded as visiting the display ground during the
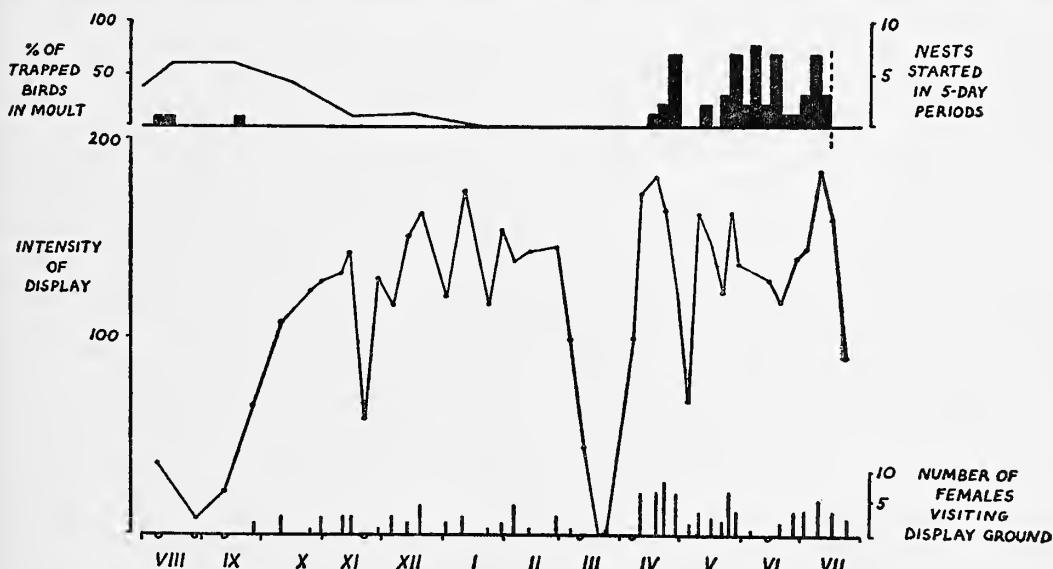
TEXT-FIG. 13. The annual cycle of display, breeding and moult, August 1958 to July 1959.

early-morning watches, the numbers of nests found in the neighboring forest, and the percentage of adults trapped in the vicinity that were undergoing wing-moult, and thus provides a conspectus of the annual cycle of the species for this one year.

It will be seen that display did not cease completely at the season of moult, but was merely much reduced. This was because individual males moulted at rather different times, so that by the time that the latest ones had abandoned their courts some of the early ones were back again. More striking was the almost complete cessation of display in the second half of March, probably due to a temporary food shortage, as discussed later. It did not occur in other years, but in 1960/61 there was a more prolonged cessation of display in December and early January, the cause of which was not clear and which also was not recorded in other years (p. 87). Thus the normally continuous cycle of display may show occasional and irregular interruptions.

Text-figure 13 also shows that small numbers of females visited the display ground from the end of the moulting period onwards, but that, as would be expected, the greatest numbers were recorded at and shortly before the start of breeding.

As shown in more detail later, the breeding season did not start at the same time in each year. In the five seasons of observation, the beginning of breeding varied from one to six months after the ending of the moult. Probably in every year the males are ready to mate over a very long period, from shortly after the end of the moult until shortly before the beginning of the following moult, and the timing of the breeding season depends on the females, whose readiness to nest is affected by environmental factors that vary from year to year (p. 87).

To settle this point, it would be necessary to make an examination of the males' gonads throughout the year. This was not a main part of the present study, but specimens were examined when available. A series of eight males, taken in the first half of December, *i.e.*, very soon after the end of the moult, had their testes well developed (mean dimensions 3.6 × 2.4 mm.; largest 5 × 3.5, smallest 3 × 2), but not so large as those of a series of nine collected in February (mean 5.2 × 3.4 mm.; largest 7 × 5, smallest 3.5 × 2.5). These birds were collected from a display ground about 12 miles east of the Arima Valley.

The Breeding Season

Text-figure 14 shows how greatly the breeding season varied in the five years. In 1957, apart from a single nest in March, breeding was first recorded at the end of May and quickly reached a peak in early June. It then continued steadily until early September. In both 1958 and 1959 breeding began abruptly in mid-April. In 1960 the start was in early January, with a single nest at the end of December, 1959, and in 1961 breeding began in the latter half of February. In all years, the start of breeding was well-defined, many nests being built and getting their eggs within a fortnight, while observations at the display ground at and shortly before this period showed intense activity resulting from the visits of numerous females, and more copulations were seen then that at any other time. There was a little evidence, as can be seen from Text-fig. 14, that nesting ended rather later in 1957 and 1958, when it began late, than in the early breeding seasons of 1960 and 1961. The breeding season lasted from 4 to 8 months in the different years.

The relation of the breeding season to weather and other environmental factors is considered in a later section (p. 85).

The Moult

Sequence of moult

The full post-breeding moult follows a sequence similar to that of other passerine birds. Replacement of the wing-feathers follows a consistent pattern. It begins with the dropping of the secondary major coverts. Typically the outer ones drop a little before the inner ones, so that as the new feathers grow they are in a graded order of length from outside inwards. While the coverts are growing, the innermost primaries are moulted, the first two or three being dropped at almost the same time. The moult of the ten primaries proceeds regularly towards the end of the wing, one feather being dropped when its neighbor on the inside is about half grown. The speed of growth of each feather is such that three adjacent feathers are generally in various stages of growth, four or only two being less usual. Like the innermost ones, the outermost two or three primaries drop at almost the same time. The moult of the nine secondaries typically begins when the primary moult has reached the 4th or 5th primary (numbered from the inside). Its sequence is less regular than that of the primaries. Secondary moult begins from the two ends and works inwards. Two or three of the innermost secondaries drop at the same time, but at the outer end of the row the second feather does not drop until several days after the first. Growth and replacement proceed more quickly from the outer than from the inner end, so that although two or three of the innermost second-
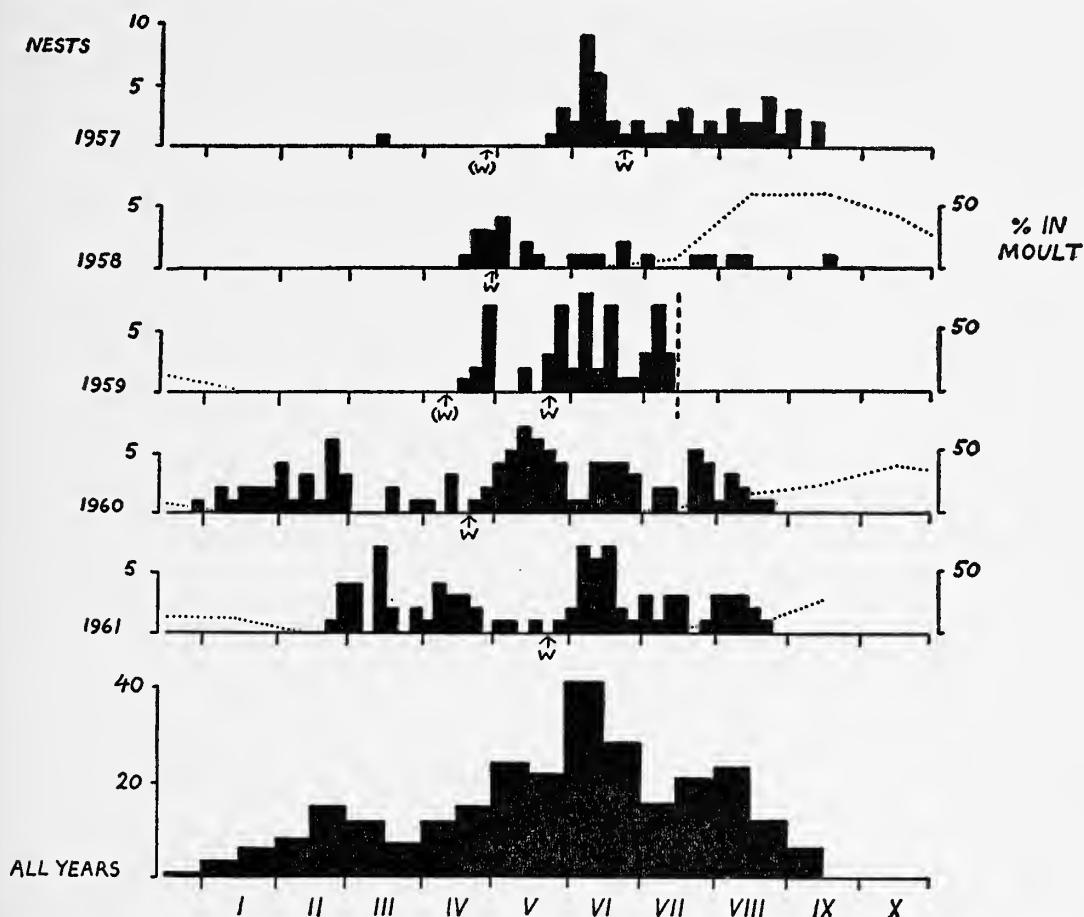
TEXT-FIG. 14. The breeding seasons, 1957-1961. Histograms: nests started in 5-day periods. Dotted lines: percentages of trapped birds undergoing wing-moult. W: beginning of wet season. (W): rainfall, followed by further dry weather.

aries drop together, the last feather to grow is usually the 5th or 6th (numbered from the outside), less usually the 4th. The moult of the tail is also less regular than that of the primaries. Typically it begins when the primary moult has reached about the 5th primary; usually all the feathers of the tail drop together and the new ones as they grow are of much the same length. The moult of the head and body is variable in its sequence, but its beginning and ending coincide closely with the beginning and ending of the primary moult and it is usually heaviest in the middle of this period.

The moult of the primaries, besides being the most regular feature, spans very nearly the entire period of the moult. The main stages of the moult have been given numbers based on the replacement of the primaries, following a method used by Miller (1961), and these numbers have been used in Text-fig. 15. The stages recognized are as follows:

Stage 1. Secondary major coverts being replaced; not primaries.
2. Primaries 1 and 2 being replaced; 3-10 old.
3. Primaries 4-10 old.
4. Primaries 5-10 old.
5. Primaries 6-10 old.
6. Primaries 7-10 old.
7. Primaries 8-10 old.
8. Primaries 9-10 old.
9. 3 or 4 outer primaries not yet full-grown.
10. 1 or 2 outer primaries not yet full-grown, or with traces of sheath at base.

The season of moult

In contrast to the breeding season, the season of moult in all probability varies very little. Text-fig. 14 shows the percentages of trapped birds
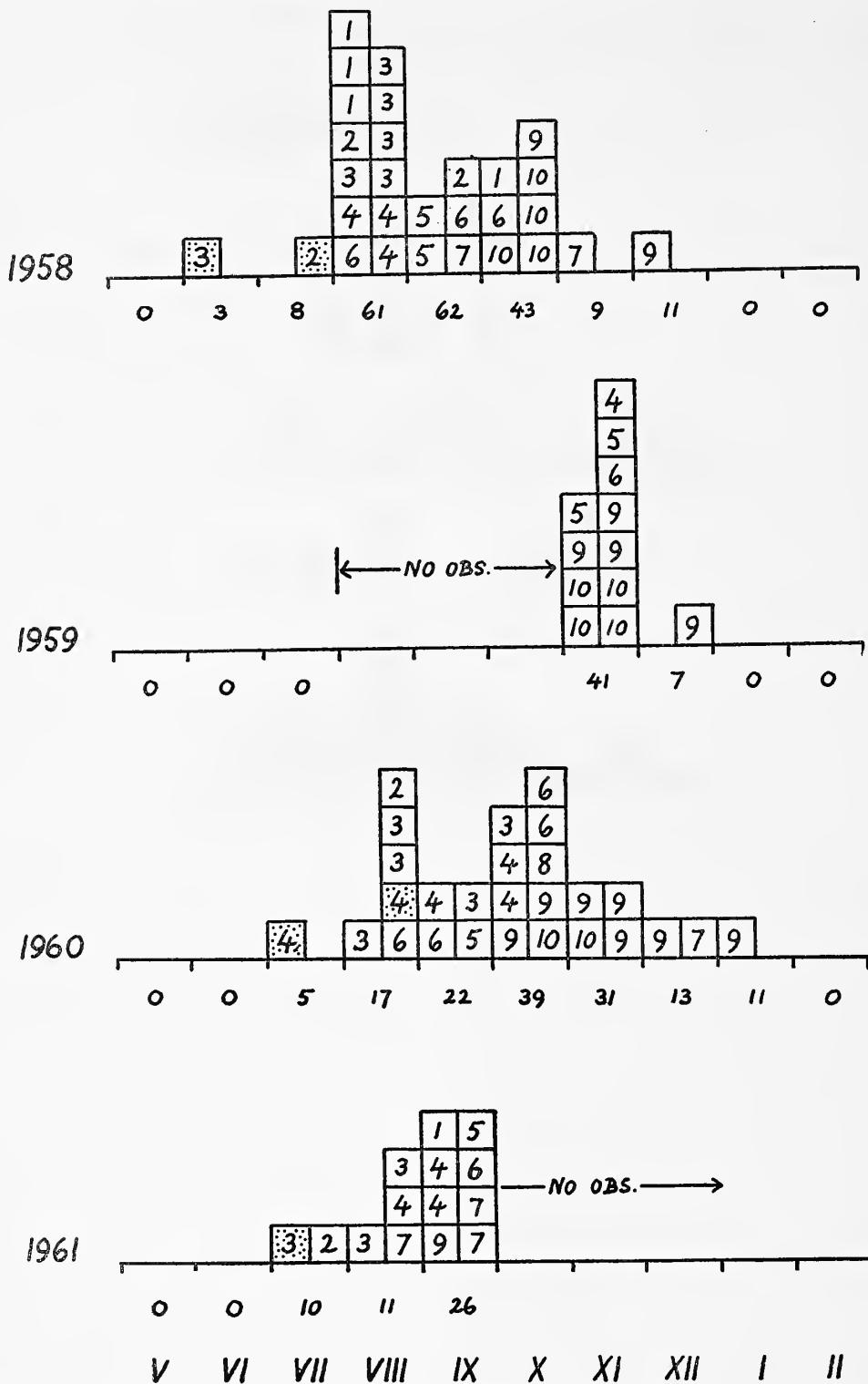
TEXT-FIG. 15. Moulting seasons, 1958-1961. Each square represents one individual trapped at the stage of moult indicated by the number. Dotted squares: juvenile males moulting into adult plumage. Figures below the line: percentages of the total number trapped that were undergoing wing-moult.

undergoing wing moult in the four years for which data were collected, and in Text-fig. 15 these moulting individuals are shown according to their stage of moult. It will be seen that the moult extends over the six months July-December, with most birds in moult in August-October. Only one individual was found to be moulting in June and one in January, and none in the months February-May. In the four years, the moult began and ended at approximately the same time.

In calculating these percentages, all trapped birds have been included. However, as will be shown later, the moult of juveniles into adult plumage, in their second autumn, takes place on average a few weeks earlier than the moult of adults. It has not been possible to separate the age-groups in Text-fig. 15, because juvenile females moulting in their second autumn cannot be distinguished from older females, but the five juvenile males are indicated.

Length of time taken to moult

The trapping of five individuals twice, and two three times, in the course of a single moult, showed that, except for the innermost and outermost primaries, two or three of which drop more or less together, the primaries drop at intervals of 8 to 10 days, and that the complete replacement of the primaries takes about 80 days. The total period from the dropping of the secondary major coverts to the completion of the growth of the last wing-feather must take a few days longer.

Observation at the display ground provided an independent assessment of the length of time taken to moult. It has already been mentioned that the males are usually present at all times except when moulting. Their disappearance before moulting and reappearance afterwards are quite sudden, and in nine cases the period of absence was known accurately to within a few days. All were between 76 and 85 days.

The moults of juveniles

Mainly in their first autumn and winter, juveniles undergo an apparently prolonged moult which is not heavy at any time, involving the head, body, lesser coverts and, at least sometimes, some of the inner secondary major coverts. All but 4 of the 35 records of this moult were in the months August to January.

In their second autumn the moult to adult plumage takes place. Unless the past history of the individual is known, this moult is recognizable only in the male, since the female and juvenile plumages are the same. What follows therefore concerns only the males.

The moult to adult plumage takes place rather earlier than the subsequent moults, being usu-

ally complete by the end of October and often by the beginning of September. The most extensive information comes from field observations of 20 young males which were seen when in juvenile plumage, most of them for the last time in June, and then again when they had completed their moult into adult plumage, at which time they are rather conspicuous as they display persistently and try to establish themselves at display grounds. Fifteen of these birds had completed their moult by the end of October, four of them as early as mid-September. It was not of course certain that they were seen as soon as they had completed their moult, so these dates are the latest possible. More exact but less abundant evidence comes from the trapping of five males during their moult into adult plumage, as shown in Text-fig. 15.

Annual variations in the moulting season

There were no obvious annual differences in the moulting season when the population was considered as a whole, but individual birds differed markedly in the times at which they moulted in different years. Eight birds were trapped while moulting in two different years (successive years, except in two cases), and one bird in three successive years. These showed considerable differences, of up to over two months, in the timing of their moults. Certainly in one case, and perhaps in two, this was due to the fact that in the first year the bird was moulting into adult plumage, but in other cases this was not so.

Observations at the display ground showed the same thing. The moulting periods of five adult males were found in two successive years, one in three successive years, and one in four successive years. These showed considerable variations from year to year which could not be attributed to the age of the bird (Text-fig. 16). The cause of these variations is considered in the next section.

ENVIRONMENTAL FACTORS AND THE ANNUAL CYCLE

In view of the annual variation in the breeding season and the relative fixity of the moult, it seems likely that the manakins' annual physiological cycle is, as it were, anchored to the yearly cycle of the seasons by their response to environmental factors initiating the moult. Consideration of the juveniles strengthens this supposition. Young birds may leave the nest in any month from January to October, yet all, as far as known, moult into adult plumage in the months June-September of the year following their year of birth.

In seeking the external regulator which year
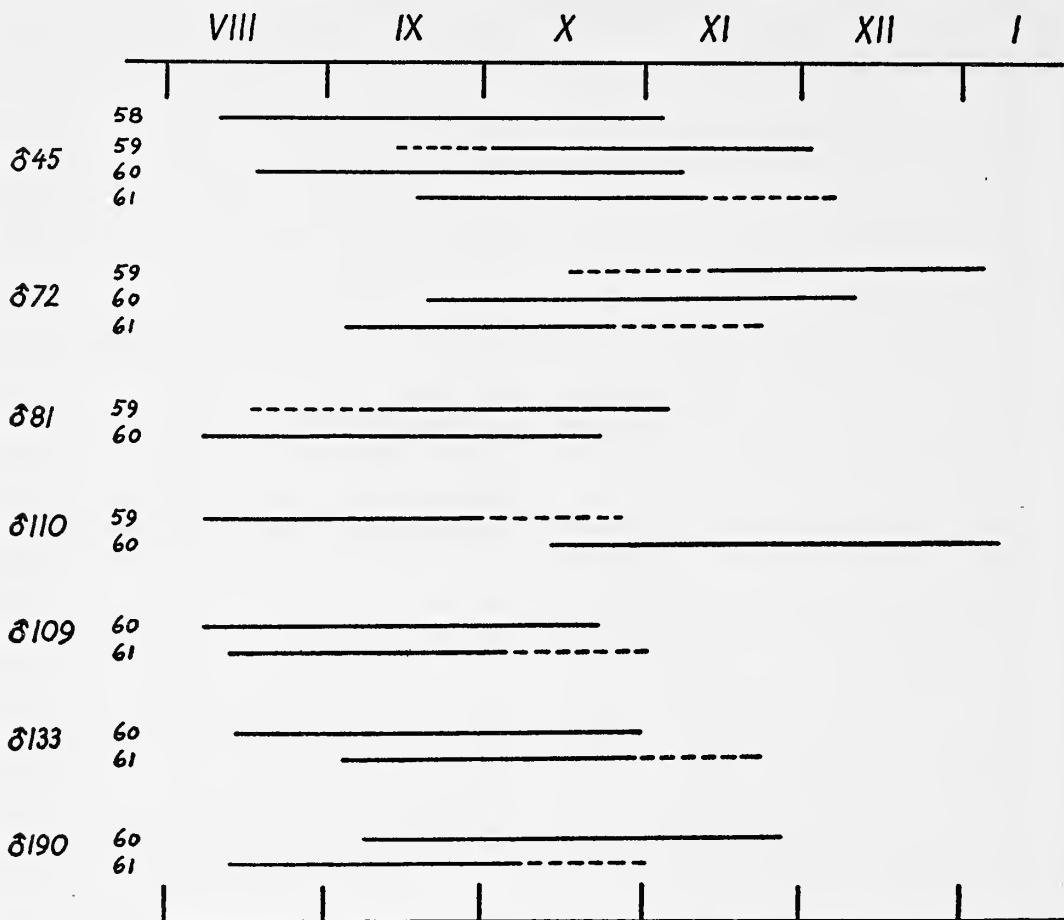
Text-fig. 16. Moulting periods of seven males in successive years. Broken lines indicate that the beginning or ending of a period was not exactly known.

after year maintains the timing of the birds' physiological cycle, keeping all the individuals more or less synchronized, we cannot consider the Black and White Manakin in isolation. Almost all other Trinidad birds, so far as known, sea birds, swamp birds and land birds, moult at approximately the same season as the Black and White Manakin (Snow & Snow, in preparation. 2). and this is of course the moulting season of northern hemisphere birds generally. It is most reasonable to suppose that the same external regulator is operating for all of them, and that this regulator is day-length, even though in Trinidad, at 10° N., the annual variation in day-length is only 74 minutes.

If day-length is the main regulator, other more variable environmental factors may still exercise important modifying or secondary effects on the timing of the different phases of the annual cycle. The data are not inconsistent with the hypothesis that the ending of the breeding

season and the start of the moult are in fact partly controlled by the onset of the wet season, though they do not follow for several weeks. The wet season began on the following dates in the four years for which there was information on the moult (parentheses indicating heavy rainfall followed by a further dry spell):

        1958–April 29
        1959–(April 9), May 22
        1960–April 20
        1961–May 22

The trapping data do not show any appreciable differences in the time of moult in these four years (Text-fig. 15), but the samples are not large and they are composed mainly of different individuals. The data on moulting dates of the same individuals over successive years show a more consistent pattern, though here again, as would be expected, there are inconsistencies. The date of moult was known for four individuals in both 1958 and 1959: all moulted

later in 1959. The dates were known for eight individuals in both 1959 and 1960: six of them moulted earlier in 1960 than in 1959. The dates were known for five in 1960 and 1961: three of them were later in 1961 than in 1960. (One individual, whose first moult was from juvenile to adult plumage, has been omitted). Thus of 17 annual differences in date of moult, 13 agreed with the differences in the date of onset of the wet season. The data for ♂ 45, the only bird whose moulting dates were known in all four years, agree exactly with the weather data (Text-fig. 16). Clearly more records would be needed, for more individuals and more years, for an adequate test, but these data are at least suggestive.

The environmental factors concerned in the onset of breeding are still obscure. Of most obvious apparent importance is the weather. The period from January to late May, during which breeding may begin, is generally dry except at the end, when heavy but irregular precipitations may occur. Towards the end of this period, in April and May, especially if there has been little recent rainfall, the ground becomes extremely parched, even in the forest, and the leaves of many herbs, shrubs and even large trees wilt. In such a case, the first heavy rainfalls stimulate many birds, including manakins, to build nests and lay eggs (as also in northern Venezuela, a short distance to the west of Trinidad; Gilliard, 1959). This occurred in 1959, when heavy rain on April 9-10 was followed by an outburst of nest-building and the first manakin eggs were recorded on April 20. But in 1957 heavy rain at the end of April had no effect, while in 1958 breeding began at the same time as in 1959 although there had been no heavy rain for several weeks. The early start in 1961 might be attributed to the weather in January and February, which was wetter than usual, but the very early start in 1960 took place before the dry season had properly begun and cannot be easily attributed to weather.

Once the breeding season has started, fluctuations in activity may be pronounced and some of these were certainly due to weather. Thus in 1961, after an early start, with steady nesting from February to the end of April, there was an almost complete cessation in May, followed by a great outburst in early June. The second half of April and most of May were exceptionally dry in this year, and it was not until May 22 that heavy rain fell.

Clearly other factors besides weather must contribute to the timing of the breeding season. Some observations suggest that fluctuations in the availability of food may play a part in some years. As will be shown later (p. 93), fruit gradually becomes more plentiful from January to April; in the first three months of the year the number of species of Melastomaceae in fruit is at its lowest, and annual variations in the fruiting seasons of the various species may result in temporary gaps, when no species is in fruit. It seems probable that such annual variations in the food supply during this period may help to determine whether the manakins start breeding early or late. The only marked food shortage was recorded in March, 1959. In mid-March there was a sudden decrease in activity at all the display grounds visited in the Arima Valley. The courts were deserted and became covered with leaves. No Melastomaceae were found in fruit—an exceptional situation, to judge from later observations—and manakins visited the guava trees in our garden and even fed on the fallen fruit. This situation lasted two or three weeks, after which display was resumed and returned to normal. As mentioned above, there was rain on April 9-10 and nesting began soon after.

In the winter 1960/61 there was an even longer period of cessation of display. Activity declined at all display grounds in December and at the main display ground under observation several males which had returned after finishing their moult disappeared again. The cessation of display by *Pipra erythrocephala* was even more complete. Display was gradually resumed during January and was normal by the end of the month. The data from the Arima Valley alone suggested a correlation between this cessation of display and food shortage. The great crop of Matchwood (*Didymopanax*) fruit, which is an important part of the manakins' food in November and December, was nearly at an end, while two important melastomes, *Miconia kappleri* and *M. myriantha,* had also recently finished, after a good crop. Another melastome of importance at this season, *M. guianensis,* was not yet ripe. There was in fact a gap in the sequence of the main fruits. However, during the same period *Pipra* ceased displaying equally completely in a locality 6 miles away on the north side of the Northern Range, in an area of forest where food was abundant. These observations emphasized the danger of generalizing from the situation in one locality only.

The problem of the start of breeding in the Black and White Manakin becomes clearer when it is considered in a wider context. There is a common pattern to which the annual cycles of most Trinidad land birds conform (Snow & Snow, in preparation. 2). As already mentioned, the months from July to October or November are occupied by the moult. After the moult,

there may be a minor peak of breeding, followed by a decline in December and then a gradual increase in breeding activity to a peak in April-June. Seen against this common pattern, the situation in the Black and White Manakin may be better understood. Immediately after the moult there is no actual breeding, though males display hard and females pay preliminary visits to the display grounds. From the end of December onwards the readiness to breed gradually increases. Early in this period of increasing readiness, especially good conditions of weather, food, or perhaps other environmental factors not obvious to the observer, are necessary to stimulate breeding. Later, nesting may be stimulated by quite slight environmental changes as long as the weather is not too dry. Towards the end of the dry season, if the drought has been severe, the onset of nesting, or its resumption after an earlier start, depends upon and follows quickly after the first heavy rainfall. Whatever the initiating factors, the start is abrupt, involving many birds at the same time, almost certainly due in part to the intense social stimulation to which manakins are exposed both at and away from the display grounds.

It must be emphasized that the details of the breeding seasons, as shown in Text-fig. 14, apply only to the Arima Valley. Visits to an area of more humid forest 10 miles to the east showed in each of three years that breeding began earlier than in the Arima Valley, in one year several weeks earlier. The difference was probably due to the different climate, and suggests a reason for the variable breeding season in the Arima Valley. Rainfall decreases steadily from east to west along the Northern Range. Concomitantly, towards the west, with an increasingly severe dry season there is an increasing tendency for birds to delay breeding until the wet season begins. In the Arima Valley, half way along the range, it appears that environmental factors favoring early or late starts are nicely balanced; hence the great variations in different years.

NESTING

The Female and her Territory

The age at which the females start to breed was not determined. Juvenile females were seen visiting display grounds when they were not more than five months old, but no information was obtained on the first nesting of a color-ringed bird. The only female of known age found nesting was nearly three years old.

Breeding females occupy small territories along the streams and gullies where most of the nests are found. Soon after the moult is over they advertise their presence by persistently call-ing the monosyllabic "peerr"; this behavior then declines, to be renewed again as the breeding season approaches. A few observations of aggressive behavior between two females at what appeared to be territory boundaries suggested that the territories are defended against neighboring females, but competition for a nesting territory does not seem to be intense. Territories are small and probably highly compressible, as occupied nests may be found within a few yards of each other. As mentioned earlier (p. 78), nests along the same stretches of stream tend to be more closely synchronized with each other than with nests along other streams, probably because the females visit the same display ground in company.

Although the females' wing-feathers are unmodified, in aggressive encounters with other females and in the presence of intruders near the nest they may give typical male displays, but with softer sounds. The beard is protruded, though the feathers are not very long, and little jumps may be made from perch to perch, each accompanied by a soft "snip." Occasionally they may make a soft "rolled snap."

Observations were made on 14 color-ringed females nesting along the section of stream that was most frequently watched, and on two nesting further afield. In general these birds remained, and so far as known nested, within the same small area during the period of observation. One bird remained in the same territory for 3½ years, and others for shorter periods. There were two known cases of change of territory. One of these birds was found nesting, within an area of about 40 by 20 yards, once in 1958, probably in 1959 (behavior suggesting nesting, but nest not found), and twice in 1960. Half way through the breeding season of 1961 (whether she had already attempted to nest or not was not known), she shifted 320 yards upstream, where she was found nesting for the fourth time. The other bird also shifted in the middle of the breeding season, in this case only 150 yards.

The Nest

The nest is built within a few feet of the ground, usually at a height of between 1½ and 5 feet. It is of typical manakin type, a rather thinly woven shallow cup, slung between horizontal supports. A large number of nests (38% of the total) were slung between two side frondlets of a fern frond, and most of the others were slung in forks between the side twigs of small saplings or shrubs. Over 95% of all the nests found were on or near the banks of streams or gullies, many of them overhanging the water.

The outer cup of the nest is made of rootlets and black fungal hyphae (probably *Marasmius* sp.; see Sick, 1957), with occasionally a few dead leaves. Some of the rootlets used are very long (29 inches in one case), and being wound round and round, inside and outside the supporting twigs, they bind the nest firmly to its support. A little cobweb is also used to secure the nest to its supporting twigs.

The lining is of different material. The great majority of all nests examined were lined with the branching panicles of *Nepsera aquatica*, a small herbaceous member of the Melastomaceae. The rich brown stalks of these panicles are very fine, smooth and shiny; each of the branches into which they are subdivided ends in a small fruit capsule. Due to the branching and to the terminal capsules, they adhere to each other when interwoven so that if pulled out the lining usually comes away from the rest of the nest intact.

Nepsera aquatica grows along forest edges and road-sides, not in the forest itself. In spite of this, it was the usual nest-lining of nests found well within the forest as well as those nearer the edges. At the main trapping place on the edge of secondary forest, six females were trapped carrying nest-material in the 1961 breeding season, and in every case it was *Nepsera aquatica*. In spite of regular searching in the neighboring secondary forest towards which they were flying when trapped, none of the nests of these six birds was found, which suggested that most of them at least were flying some distance with the nest-material, as indeed it is clear that many birds must which nest far from a forest edge. No birds were trapped carrying nest-material in other years, suggesting that *Nepsera* was unusually scarce elsewhere in 1961.

Unfortunately the identity of the nest-lining was not discovered until late in the study. Incomplete observations made subsequently suggested that *Nepsera* flowers mainly in the dry season, from December to April, and that the dead or fruiting panicles are mainly available from March to August. In support of this suggestion, it was several times noted that early nests were lined with other less suitable material, sometimes finely branched dead grass-heads. But observations on this point were inadequate to show whether the availability of *Nepsera* could be a factor in the timing of the breeding season, and the point requires further study.

For three nests an interval of four days was recorded between the beginning of building (a few strands only in place) and nest completion, and for seven others intervals of 5-7 days were recorded. Nests sometimes remain half completed for days, apparently because the female is not ready to lay.

INCUBATION AND FLEDGING

Detailed observations from a hide were made at only one nest. These are the basis of the account of behavior at the nest given here. The rest of the data in this section were obtained in the course of repeated visits to many nests.

The clutch, normally of two eggs, is usually laid soon after the nest is complete. In every case in which there was information on the point, the second egg was laid two days after the first. Though visits were not usually frequent enough to give an exact time of laying, the time of laying of eleven eggs was known within a few hours and all were laid round the middle of the day, mostly between 1000 and 1400 hours, none being earlier than 0750 or later than 1545.

Apparently complete clutches of one egg are not rare. The clutch was regarded as complete when the number of eggs present remained the same for three days or more and the bird was known to be incubating. Of the 244 complete clutches thus recorded, 22 consisted of only one egg.

The female does not usually sit until the second egg is laid. Thereafter she is regularly on, except for periodic absences during which she must feed. At the nest under observation from a hide, during three hours' watching in the morning in fine weather, three days before the eggs hatched, the female sat for 71% of the time. Two completed periods on the nest lasted 46 and 53 minutes, and two recesses lasted 14 and 26 minutes. As incubation proceeds, the female sits more and more tightly. Early in incubation she usually flies from the nest when the observer is still several yards away; in the last two or three days before hatching she usually remains on the nest until the observer is very close and then flutters away close to the ground giving distraction display.

The incubation period (from the laying of the second egg to the hatching of the second young) was ascertained at seven nests to be 19 ± ½ days and at two nests to be 18 ± ½ days.

The young hatch with a thin covering of down. At the nest under observation, when they were one day old they were brooded for 34% of the time during a watch of nearly two hours in the morning. When they were five days old they were brooded for 41% of the time during a watch of one hour 40 minutes, but the next day they were not seen to be brooded at all. They are generally very silent. Small nestlings utter soft cheeping calls audible for only a few feet; no calls were heard from large nestlings.

The young are fed by regurgitation, mainly on fruit with a small proportion of insect food. The bird under observation from a hide normally arrived with no food in the beak, perched on the edge of the nest, and produced a succession of fruits which she would give to the two young alternately. The feeding rate was recorded on five days and showed a steady increase, from one feed every 28 minutes when the young were one day old to one feed every 18 minutes at 13 days.

Like the adults, the nestlings are capable of swallowing surprisingly large fruits. At the nest under observation, some of the fruits brought to the young were not only very large but consisted mainly of a large seed only partially enclosed by a small aril. After swallowing the fruit the young regurgitate the larger seeds, and nests with young are often found to have one or two seeds lying in the nest-cup. At the nest under observation, the female picked up these seeds and usually swallowed them, but occasionally carried them away. She also swallowed the faeces of the young up to the tenth day; on the thirteenth day she sometimes swallowed them, and sometimes the young defaecated over the nest-edge.

Thus as the young grow larger an accumulation of regurgitated and defaecated seeds, together with a few insect hard-parts, spatters the ground and leaves below the nest. Examination of many of these piles of remains, as well as observations from the hide, showed that the young are fed on the same fruits as the adults themselves eat, except for some of the largest kinds.

The young remain in the nest for 13-15 days. For six nests with two young the periods were: 13 and 14; 14; 14; 14; at least 14; 14 and 15 days. For two nests with one young the periods were 13 and 14 days.

After they have left the nest the young are extremely difficult to see. They perch in low vegetation, move little, and either do not call or call very seldom. Later they accompany the female but are still not easy to locate because they are so silent. It was remarkable that the juvenile's begging call, a loud and distinctive "weeee-e-e," rather plaintive and slurred at the end, was only heard on one occasion, from two full-grown juveniles accompanying a female. Thus little information was obtained on the post-fledging period by direct observation, but data on the interval between the fledging of young and the start of the next clutch (Table V) suggest that the young are attended by the female for three or four weeks.

Breeding Success and Reproductive Rate

In calculating nesting success, only those nests have been used that were found before the clutch was complete; most were in fact found while they were being built. (For a discussion of the bias introduced if nests found at a later stage are included, see Snow, 1955). In this way we can obtain figures for the percentage of all nests started (*i.e.*, in which eggs were laid) that reached the hatching and fledging stages, and for the number of young produced for each nest started. Table II summarizes the results of the five seasons' observations.

Like other tropical forest birds (Skutch, 1945), *M. manacus* has a very high rate of nest failure. Combining all the years, 40% of all nests started reached the hatching stage, and 19% produced fledged young; each nest started produced an average of 0.33 fledglings. There were considerable differences between the years, but the significance of these is uncertain. Analysis by months shows that late nests were considerably more successful than early nests (Table III).

Most nests fail early, apparently through predation (Table IV). Predation also falls heavily on the 40% that reach the nestling stage. In all, 86% of all nest losses were attributed to predation. In nearly every case predation can only be presumed, as there was no evidence except a clean, empty nest. Indirect evidence suggests that the chief predators are snakes, of which there are several known or potential egg-

TABLE II. BREEDING SUCCESS

Year	Number of nests	Reached hatching	Reached fledging	% reaching fledging	Number of young fledged
1957	29	18 + 3?	12	41	22
1958	19	3	3	16	5
1959	30	7 + 2?	4	13	8
1960	79	39 + 11?	18	23	28
1961	70	13 + 6?	7	10	11
All years	227	80-102	44	19	74

Note. Queries in the hatching column indicate that the nest failed just before or just after hatching, the exact time not being known.

TABLE III.
ANALYSIS OF BREEDING SUCCESS BY MONTHS

Month	Number of nests	Reached fledging	Number of young fledged	Number of young per nest
Jan.	6	0	0	}0.14
Feb.	16	2	3	
Mar.	14	2	4	}0.13
Apr.	34	2	2	
May	43	10	17	}0.35
June	63	11	20	
July	25	9	15	}0.55
Aug.	26	8	13	

eating species frequenting low growth in the forest. The fact that no traces of chewed egg shell were ever found in or near a nest seems to rule out small mammals as important predators. Neither have birds been implicated. The toucan *Ramphastos vitellinus,* the only Trinidad representative of a family known to be nest-robbers (Skutch, 1944), rarely comes within 20 feet of the ground. The large cacique *Psarocolius decumanus* and the larger flycatchers may occasionally rob nests, but there was no evidence that any of these could be important nest-predators near ground-level in the forest.

Frequently nests are found not only empty but partly dismantled only a day or two after they had been occupied. This is not however due to a predator. The nest-material is much in demand, not only by other manakins but by the flycatcher *Pipromorpha oleaginea,* so that abandoned nests may soon be reduced to a mere framework.

Inadequate construction or support of the nest caused 6% of all the failures. In particular, nests are sometimes slung between side-fronds of a fern which after a time wither, so that the

TABLE IV. CAUSES OF NEST FAILURE

Cause of failure	Number of nests
Eggs predated	105
Eggs deserted	3
Eggs lost through collapse of nest	11
Eggs or small young predated	24
Young predated	29
Young lost through collapse of nest	1
Nest flooded	7
Tree fell on nest	1
Human disturbance	2

nest tilts and the eggs or young fall out. Natural catastrophes were the only other regular cause of failure (4% of the total); in several cases nests placed low over streams were flooded or swept away after heavy rain, and once a nest was destroyed by a natural tree-fall. Loss by flooding was the only cause of failure which showed seasonal variation; all cases occurred in the wet months June-August.

Reproductive rate

Individual females nest more than once in the course of the long breeding season, but it is not easy to find out the average number of nesting attempts made by each bird. Observations at the display ground showed that known females visited and displayed with the males at intervals throughout the beeding season, but were too few to throw any certain light on how many times a single female attempted to nest in the season. More satisfactory information comes from observations on the repeated use of the same nests.

As already mentioned, the females usually occupy fixed territories throughout the breeding season. Thus when a nest is used more than once, or when a new nest is built within a few feet of the site of a previous one, it is likely that the same female is involved. Also, in such cases the intervals between the ending of one nesting attempt and the laying of the next clutch show certain consistencies (Table V), which further supports the belief that the same bird is involved. Fortunately, repeated use of the same nest or nest-site is rather common.

TABLE V. INTERVALS BETWEEN BROODS

	Number of days between end of one breeding attempt and laying of first egg of next clutch				
	0-10	11-20	21-30	31-40	41+
After loss of eggs or young	4	10	5	5	7
After successful fledging	—	—	3	4	1

In 1957 and 1958, when the breeding seasons were rather short, 11 nests or nest-sites were used twice. In 1960, with a very long breeding season, 12 nests or sites were used twice, 3 three times, 2 four times, and there was a single case of a succession of five nestings in two nests, the second nest, which was used twice, being built within a few feet of the first, which was used three times. In 1961, with a fairly long breeding season, 11 nests were used twice and 3 three times.

These observations suggest that two to four nesting attempts during the breeding season are usual, two being commoner in a short season and three or four occurring more often in the longer breeding seasons. If three is provisionally accepted as the average number, then, with each nest started producing on average 0.33 fledglings, each female will on average rear approximately one fledgling a year.

In the years 1957-60 15 nestlings were ringed along the section of stream where intensive trapping was carried out, and all, as far as known, left the nest successfully. Of these, four were later trapped and became fully adult (*i.e.*, reached their second autumn) and a fifth was seen several times, up to nearly a year after it had left the nest. The other ten were never trapped nor seen. Though a small sample, this suggests that at least one-third of the birds which leave the nest survive to become adult. Thus if each breeding female rears on average one fledgling a year, she will contribute on average 0.33 to the next year's adult population.

FOOD

Feeding Habits

The Black and White Manakin is predominantly a fruit-eater, taking a great variety of fruits from trees, shrubs and even low herbs. Typically the bird makes a rapid sally from its perch, plucks a fruit in flight, lands with it in its beak, and then swallows it whole. But fruits are sometimes plucked from a perched position if they are accessible. Manakins do not hop about to feed, nor do they cling to the bunches of fruit on which they are feeding, as do the tanagers and honeycreepers which are often seen feeding with them.

Almost all the fruits eaten are small berries, but a few exceptions were noted. Sometimes pieces are plucked from the fruiting catkins of *Cecropia peltata,* sections are taken from the compound fruit of the introduced rubber tree *Castilloa elastica,* and during the period of food shortage mentioned earlier manakins came down onto the ground and fed on fallen fruits of the cultivated guava (*Psidium guajava*).

They have a wide gape and can swallow very large fruits for their size. They often have to "juggle" large fruits in the beak for some time before they can swallow them; probably the fruit is softened during the process and so made easier to swallow. With the largest fruits of all, this juggling may go on for a minute or more, while it seems to the observer that the bird cannot possibly succeed in getting the fruit down. The three largest fruits that manakins were seen eating, after much juggling, were the following:

Coussarea paniculata (Rubiaceae), length 19, diameter 16 mm.; *Protium guianense* (Burseraceae), length 15, diameter 11 mm.; and *Cordia lockhartii* (Boraginaceae), length 15, diameter 10 mm. Undoubtedly the wide gape is of great importance to the species in making available a greater range of fruits than could normally be eaten by such small birds. Thus Black and White Manakins can feed on fruits that cannot be eaten by considerably larger birds such as the tanagers *Tangara mexicana* and *T. gyrola.*

A small quantity of insect food is taken, also in flight. Not uncommonly manakins follow army ants and take the insects disturbed by them, plucking them in flight from a leaf or tree trunk. Occasionally a manakin is seen, when feeding on berries, to pluck a small object, probably a resting insect or spider, from the underside of a leaf. When termites swarm after the heavy rains which bring the dry season to an end, manakins hawk for them from exposed tree-top perches, as do many other birds.

A greater proportion of insect food is fed to the young than is eaten by the adults themselves. Thus insect remains were found in eight of 15 food samples collected from below nests with young, but in only four of 93 samples collected from display grounds. Nearly all the insect remains consisted of hard parts of the imagines of small Coleoptera and Diptera; remains of a small damsel-fly (Odonata, Zygoptera) were also found in three of the samples. The fact that insect larvae were never found in the samples may not be significant in itself, as they would probably not be distinguishable among the food debris. However, the birds' behavior when feeding suggests that they would rarely be taken.

Black and White Manakins drink regularly from the water that collects in the large colored bracts of the abundant banana-like plant *Heliconia* cf. *wagneriana.* Less often, they drink from streams.

Composition of the Food

Altogether, Black and White Manakins were seen feeding on the fruits of 66 species of plants (40 trees, 13 shrubs, 7 vines, 6 others), of which 4 (3 trees, 1 vine) remained unidentified. Collections of seeds from display grounds and below nests brought the total to 105 species, of which 32 remained unidentified. Most of the unidentified species were represented by only a few seeds, and comprised a very small fraction of the total food. The identified fruits, and the months in which they were found to be eaten, are listed in Appendix 2.

As already noted, one family of plants, the

Melastomaceae, is of especial importance. 47% of all records of manakins observed feeding were from Melastomaceae. All except nine of the 108 samples collected from display grounds and below nests contained melastome seeds, which often far outnumbered everything else; seven samples contained only melastome seeds. Records were obtained of manakins feeding on at least 17 species of melastomes, nearly all of them trees and shrubs of the genus *Miconia*. Several other less common species were probably fed on. The berries of these melastomes contain large numbers of very small seeds which show little difference between the species. Except for one species with unusually large seeds, they were not distinguished in the samples collected from display grounds and below nests.

The family Rubiaceae was easily second in importance to the Melastomaceae. At least 15 species of this family were found to be eaten, and 14% of all observations of birds feeding were from them. The remainder of the identified food plants belonged to a variety of families, with few species in each. The Euphorbiaceae and the Moraceae, both with 4 species, were the most important tree families in number of species. The greatest number of records for single tree species were from *Didymopanax morototoni* (Araliaceae) and *Ficus clusiifolia* (Moraceae).

Records were obtained from a variety of smaller plants, the only apparent requirement being that they should bear fleshy berries of the right size. Among these were aroids of the genera *Monstera* and *Philodendron, Costus spiralis* (Zingiberaceae), *Stromanthe tonckat* (Marantaceae), two species of *Heliconia* (Musaceae) and the grass *Lasiacis sorghoidea.* There were no records of manakins feeding on the fruits of aroids of the genus *Anthurium,* the epiphytic cactus *Rhipsalus,* or any of the mistletoes. They are all common, and were fed on by some other fruit-eating birds. They are translucent berries, with a rather tough skin enclosing a sticky pulp, and perhaps are not easily digestible by manakins.

The Melastomaceae.—Trees and shrubs of the genus *Miconia* are a conspicuous feature of the secondary vegetation of the Arima Valley. They also occur, but not so abundantly, in primary forest. They range in size from shrubs a few feet high to 70-foot trees, but apart from their size they are all rather similar in appearance and all bear, in conspicuous terminal panicles, roundish berries which are from 3 to 10 mm. in diameter and contain numerous very small seeds embedded in pulp. Three other genera of melastomaceous shrubs, *Clidemia, Conostegia*

and *Platycentrum,* have similar fruits, but as food for manakins, at least in the study area, they were of minor importance. There was also one record of a manakin picking pieces from the much larger fruit of a melastomaceous tree of the genus *Henriettea.*

In the Arima Valley trees of the genus *Miconia* produce a constant succession of fruit throughout the year (Text-fig. 17). A greater number of species are usually in fruit in the wet than in the dry season (Table VI), so that the food supply then is more assured. Two of the commonest species, *M. guianensis* and *M. multispicata,* fruit in the dry season, and one or two others of lesser importance, but annual variations in their fruiting seasons can produce a temporary gap in the succession. As already mentioned, this apparently happened in March, 1959, but unfortunately the different species had not been distinguished by then and it was only recorded that no melastomes could be found in fruit. There was also a gap in January, 1961, when *M. kappleri* and *M. myriantha* had just finished fruiting and *M. guianensis* had not yet ripened.

The shrubs of the genus *Miconia,* as well as those of the related genera mentioned above, are of far less importance, only 4% of all the records from melastomes being from them. They tend to fruit less prolifically than the trees and to spread their fruiting over a longer period. Thus few berries are available on one plant at one time, and manakins do not pay much attention to them when the more abundantly fruiting trees are available. They fruit more in the wet season than the dry (Table VI).

The Rubiaceae.—In the forest a large number of the small trees and shrubs belong to this family. The identification of some of them is not easy, and a few more than the 15 recorded species may have been involved. Like the melastomes, many of them bear fruit conspicuously in terminal panicles. Their fruits are more diverse in appearance, many of them being rather larger than those of the melastomes. They contain in most species one or two, in a few species several, seeds embedded in pulp; some species have arillate fruit. Like the melastomes, the tree species have mainly well-defined fruiting seasons, while the shrubs fruit over a long period but mainly in the wet season. Thus they also provide a more or less continuous food supply throughout the year, but far less abundantly than the Melastomaceae.

AVAILABILITY OF FOOD THROUGHOUT THE YEAR

Text-figure 18 shows that there were well-marked seasonal changes in the numbers of

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII

M. multispicata

M. splendens

M. tomentosa

M. prasina

M. amplexans

M. chrysophylla

M. affinis

M. kappleri

M. punctata

M. myriantha

M. holosericea

M. guianensis
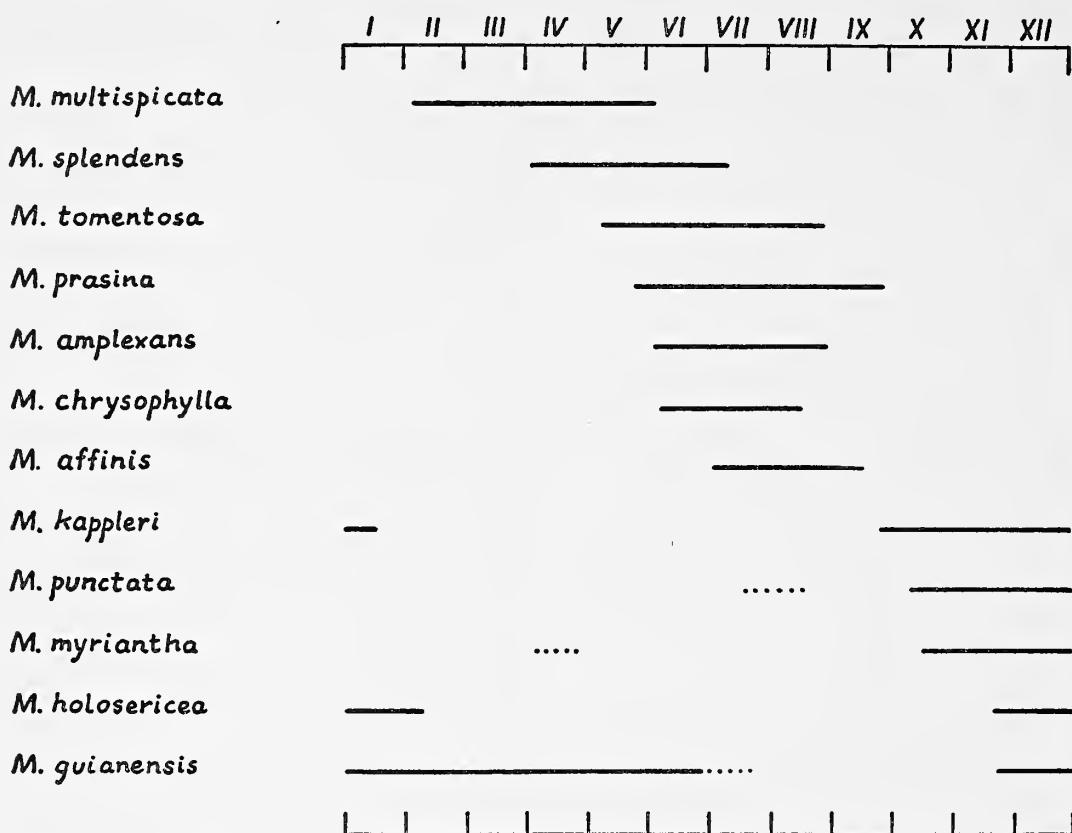
Text-fig. 17. Fruiting seasons of *Miconia* tree species, Arima Valley, October 1959 to September 1961. (Since most of the species did not fruit at exactly the same time in the different years, the fruiting periods for any one year were mostly a little shorter than shown.)

kinds of fruit recorded as taken in the different months, with a marked peak in April and a minor one in November-December. But the high figures in the period February-July are partly caused by the inclusion of samples collected from below nests, which included various small seeds not found at the display grounds and perhaps taken because the small berries containing them were specially suitable as food for nestlings. A truer picture of the variety of food available is probably presented by Text-fig. 19, which shows the average number of different kinds of fruit in the collections made at display ground A, and thus eliminates variation due to locality and the requirements of nestlings. Again

the figure shows that there was a steady increase in variety from January onwards, with the greatest variety between March and June and the least from August to October.

It has already been shown that the date at which breeding starts is variable, ranging from early January to late May. In relation to the food supply, it starts at some time in the period when the variety of food available is steadily increasing. Food conditions are by no means the same in each year, and it seems reasonable to suppose that their variation may affect the time at which breeding starts.

Though no quantitative assessment of insect food has been made, it appears almost certain

TABLE VI. NUMBER OF SPECIES OF MELASTOMACEAE IN FRUIT IN DIFFERENT MONTHS

	Jan.	Feb.	Mar.	Apr.	May	June	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Trees	3	3	3	3	5	8	7	5	3	4	6	6
Shrubs	—	—	—	—	2	4	4	5	5	5	3	1

Note. Especially in the shrubs, there is a little out-of-season fruiting. This has been omitted; figures indicate regular and abundant fruiting.
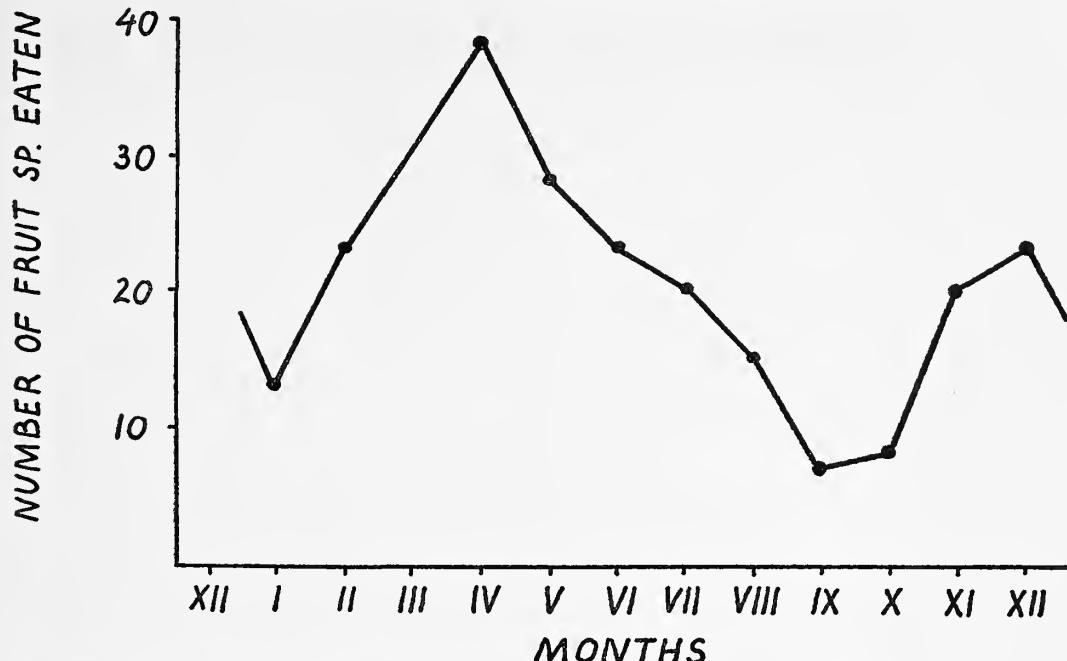
TEXT-FIG. 18. Total numbers of fruit species found to be eaten throughout the year.

that insects are available in greatest numbers in the early part of the wet season. It is then that termites swarm, mosquitoes increase, and most Lepidoptera are breeding. Thus the early part of the manakins' breeding season probably coincides with the period of greatest abundance of insects as well as fruit. By the time that breeding ceases, in August and September, the variety of fruit is decreasing and approaching its minimum.

Although temporary, perhaps local, food shortages may occur, it seems that for the Black
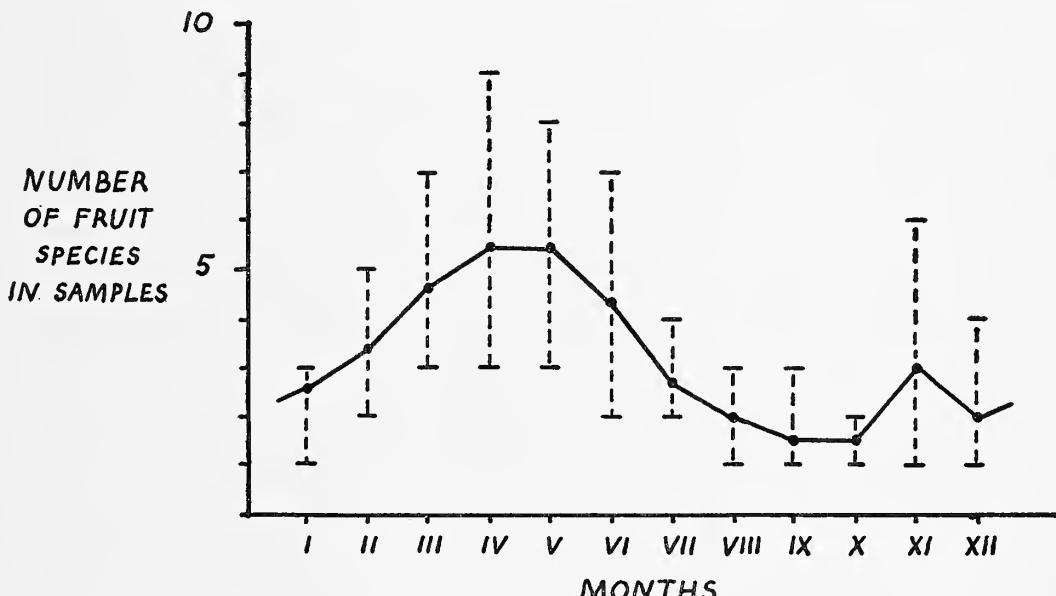
TEXT-FIG. 19. Number of fruit species in food samples collected from display ground A, showing the range (broken line) and the mean.
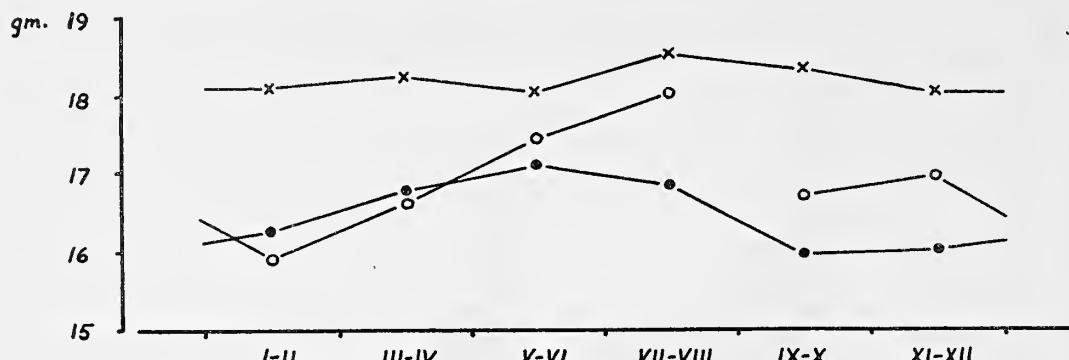
TEXT-FIG. 20. Mean weights of adult males (crosses), juvenile males (open circles), and females (dots), grouped in two-monthly periods. (From the data given in Appendix 3.)

and White Manakin there is no regularly recurring period of food shortage such as plays such an important part in the ecology of northern birds. This is of course what might be expected; the generalization has often been made by writers on tropical forest birds, without the support of detailed data. For the Black and White Manakin, the evidence from an analysis of the food, given above, is further supported by observations at display grounds and from the weights of trapped birds.

As already mentioned, adult males can feed themselves in less than 10% of the daylight hours. And the food collected in this short period suffices for regular bouts of intense activity at the court. This applies to all months of the year, since even at the height of the moult some early or late individuals are usually present at the display grounds.

Analysis of weights lends further support. All known birds which undergo annual periods of food shortage lay down in advance reserves of fat to meet the shortage (Lack, 1954). But adult male Black and White Manakins showed no significant variation in weight throughout the year (Text-fig. 20). Adult females showed a seasonal change in weight that was certainly due to enlargement of the ovary and development of eggs, and juvenile males showed a seasonal increase in weight that was attributable to the gradual development of the muscles involved in display, bringing them up from the juvenile to the adult male weight. The full data are given in Appendix 3.

When weights of adult males and of females from all months are combined (Text-fig. 21), both show a similar frequency distribution, with a long "tail" towards the upper end of the scale and very few individuals at the lower end. This suggests that during the period of the study few individuals in the population could have been undernourished or subnormal. It is significant that none of the 38 color-ringed males that were under observation at the display grounds died during the two periods of temporary food shortage.

THE ANNUAL SURVIVAL OF ADULTS

Because adult males normally retain their courts indefinitely, once they have settled down, it is comparatively easy, by observing color-ringed males at display grounds over a long enough period, to find the annual mortality. The figure so obtained must of course be a maximum, since if a bird shifts its court to another display ground it may not be found again and will be recorded as dead. In fact this source of error is almost certainly not serious in the present case. Only one adult male was known to have shifted to another display ground and it had spent a year without establishing itself at the first display ground (p. 80). Of the established males which disappeared from display grounds, none was ever seen or trapped again, so it was probably correct to assume that they were dead.

The annual survival of each male was assessed from the date on which it was first found to be established at a court. If it survived to the same date on the following year, its further survival could again be assessed. The only male ringed early enough to give evidence of survival over three years did in fact survive. Several males survived for the two years for which their survival could be recorded. On this basis, the survival of 38 color-ringed birds was available for analysis, giving a total of 56 records of survival from one year to the next. The results, given in Table VII, show that the annual survival of these males was 89%.

The annual survival of adult females could not be assessed in the same way. Though they
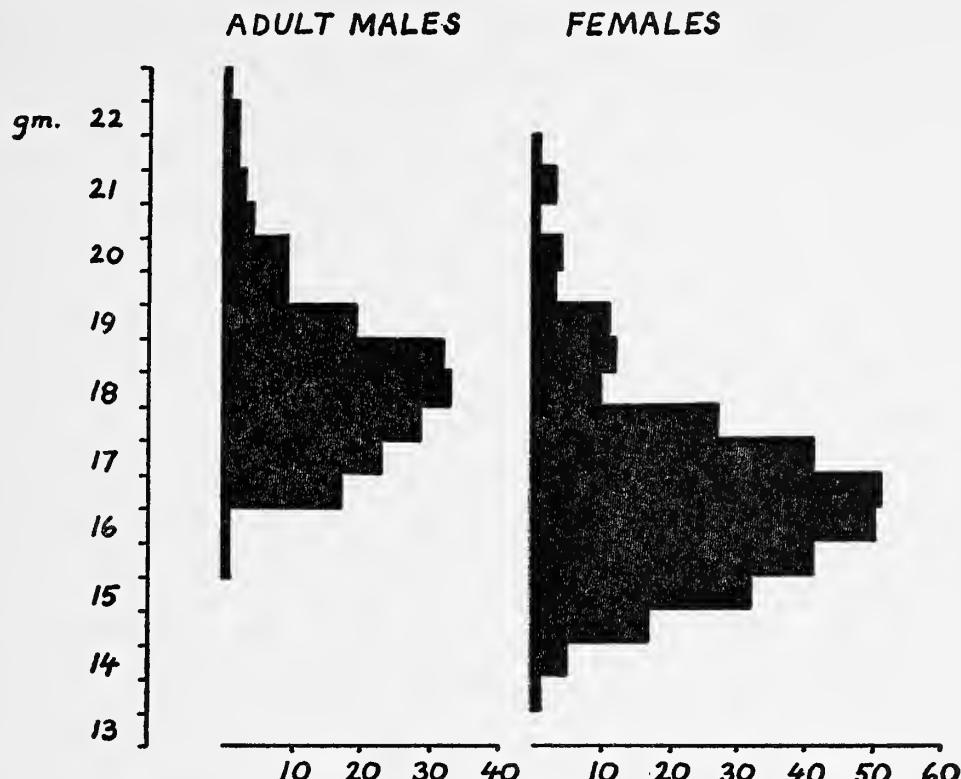
TEXT.-FIG. 21. Combined weights of all adult males and females, all months.

hold breeding territories, these are shifted more often than the males' courts, and the disappearance of a female from a small area could not be taken as evidence of death. However, the trapping data showed a high rate of survival. Thus of the first eight females trapped, in June, 1958, one was never retrapped nor seen again, but the other seven were known to have survived for an average of over 2½ years, five of them being alive at or shortly before the time when observations ceased, in September, 1961.

The trapping data also showed that the sex ratio of the adults was equal or nearly so, which implies that the females' survival rate must be about as good as the males'. Table VIII gives an analysis of the first 100 birds trapped at a feeding area away from the display grounds. Forty-two of them were males, 40 of them females,

and the sex of 18 birds in female or juvenile plumage was not determined. This last category must have consisted of juvenile males, and adult and juvenile females, the females preponderating as they included two age-classes. The sex-ratio of this sample must therefore have been near 50:50. The figures for the second hundred are similar, except that the undetermined category was greater as there was not so much time for subsequent observation and retrapping (known males 40, known females 35, undetermined 25).

An annual survival of 89% is far higher than that of any other small bird whose survival rate is known (Lack, 1954). But very high survival rates may well be general in tropical forest birds. If, as seems usual, their reproductive rate is very low, it follows that their annual survival must

TABLE VII. ANNUAL SURVIVAL OF ADULT MALES

Ringed early enough for survival over one year to be recorded: 38	Number surviving: 35
Ringed early enough for survival over 2nd year to be recorded: 17	" " 14
Ringed early enough for survival over 3rd year to be recorded: 1	" " 1
All observations: 56	" " 50

TABLE VIII. ANALYSIS OF SEXES OF TRAPPED BIRDS
(First hundred individuals trapped at feeding and
bathing places away from display grounds)

Trapped as adult males	28
Trapped in female/juvenile plumage:	
later known to have been males	14
later known to have been females	40
sex not determined	18

be high. For the Black and White Manakin the figures for reproductive rate and survival balance as well as could be expected. With 89% annual survival, if the population is to remain stable each female must contribute annually an average of 0.22 adults to the next year's population. This figure is reasonably close to the 0.33 independently estimated for the reproductive rate (p. 92).

DISCUSSION: THE EVOLUTION OF COMMUNAL DISPLAYS

Advertisement and courtship displays of males have evolved to an extreme degree in many species of tropical forest birds—especially hummingbirds, cotingas, manakins, bowerbirds and birds of paradise. In several species of manakins, a few hummingbirds and cotingas, and at least one bird of paradise, communal or "lek" displays have been evolved. Such behavior is of course known in birds of other habitats (*e.g.,* Ruff *Philomachus pugnax* and species of grouse), yet there can be no doubt that the tropical forest environment is especially favorable to the evolution of elaborate group displays.

The present study throws light on the ecological factors favoring communal display in the Black and White Manakin. To apply the conclusions reached here beyond this species and other small manakins would be rash; nevertheless it is probable that similar ecological circumstances have been important in the evolution of the sexual behavior of the other tropical forest families mentioned above.

In the Black and White Manakin we find the following. The food supply is rather uniform throughout the year, with no regular period of food shortage. Normally an individual can satisfy its food requirements in a very short time in each day (at most, 10% of the daylight hours). The breeding season is long, and variable in its time of onset. Clutch-size, and consequently family-size, is low, and it seems unlikely that a female normally finds it difficult to supply the needs of one or two young ones. Nesting success is very low, most of the losses being due to predation. The expectation of life

of the adult is very high compared with that of other small birds whose mortality rate is known.

The manakins' low clutch-size cannot be regarded as in any way consequent on its special way of life. Almost all other species building open nests in the same habitat also lay a clutch of two eggs (see also Skutch, 1949). I agree with Skutch in attributing the low clutch-size of birds in tropical forest mainly to the high rate of predation, which gives a selective advantage to nests which need visiting very seldom and are as inconspicuous as possible. The problem is essentially a quantitative one, whether on average more, or fewer, young would be reared if the clutch were larger. As yet, neither for manakins nor for any other tropical forest bird are there critical data enabling the hypothesis to be tested. For the present argument, however, the importance of the low family-size is that it is one of the ecological prerequisites for the evolution of the manakins' communal display.

Where nest predation is heavy and clutch-size low, the emancipation of the male from attendance at the nest presents obvious advantages, especially if he is more brightly colored than the female. This is possible if the female does not need much time to find food for herself and her family. Thus her absences from the nest during incubation need not be long, and when the eggs hatch she will have no difficulty in feeding two nestlings as well as herself. Selection will thus favor the progressive dissociation of the male from the care of the nest and young.

Once the male is free of nesting duties, the pair bond can be broken and he becomes free to mate with as many females as he can attract. Thus sexual competition between the males will intensify, and selection will promote the development of all structures and behavior enhancing the effectiveness of the male's display. The ability to find food quickly will enable the male to devote a great part of his time to attracting prospective mates. If the female's breeding season is a long one, natural selection will ensure that the male's period of display is at least as long.

Probably the fundamental requirement is a food supply which enables the individual to get its nourishment in a short time in each day. Thus the manakins, and those cotingas and birds of paradise with similar behavior, are all primarily fruit-eaters. No primarily insectivorous groups have evolved along these lines. Of the huge family of New World flycatchers (Tyrannidae), which includes many species inhabiting tropical forest, one species, *Pipromorpha oleaginea,* is known to have evolved this kind of behavior (Skutch, 1960; personal obs.): the males spend most of their time calling and displaying in fixed

places in the forest and take no part in the nesting. Of all the small flycatchers observed in the Arima Valley, this was the only species found to eat fruit regularly; Skutch has recorded that fruits are also fed to the young. The mainly nectarivorous hummingbirds, whose communal displays are highly developed, can also feed themselves in a very short time in each day (Snow & Snow, in preparation. 1). Once this requirement is met, the emancipation of the male from the nest becomes possible and all further developments can follow.

Whether or not evolution leads to communal or "lek" displays depends on other factors. Thus the bellbirds are sexually highly dimorphic and the males spend much of their time in display, but they display in scattered groups within earshot but not within sight of each other (B. K. Snow, 1960), and in some manakins the situation is similar. But the bellbirds have extremely loud calls and can advertise their presence to females a long way off. For a small bird in thick forest, traditional display grounds, which the females know and can visit when they are ready to mate, are an obvious advantage. Almost certainly, however, this is not the main advantage of a lek over a solitarily displaying male. A single manakin displaying at a solitary court in the forest would soon become known to the local females and they would have no difficulty in finding him. Other species of manakins have display perches well apart from their fellows. The crucial point is that a group of males displaying together must have a much greater attraction for the female and a greater stimulating effect on her, once she has arrived, than a solitary male. Otherwise it would seem advantageous for males to display at some distance from their fellows, where competition for the attention of the female would be less intense.

If the conspicuousness of males at communal display grounds made them more liable to predation, we should have an important selective factor working against the evolution of communal displays. But the evidence for the Black and White Manakin is against such a hypothesis, as the annual survival rate of males with courts is extremely high and probably nearly the same as that of the females, which are far less conspicuous.

Strong sexual selection will lead to the extreme development of display structures and exaggerated display movements, and as Sibley (1957) has pointed out, the more distinct the displays and structures are in related species, the more effective they will be as isolating mechanisms. But the extreme ritualization of the display movements probably has another important function. In a species in which no pair bond is formed, the female has no opportunity to become acquainted with her mate over a long period. Ethological studies have shown the importance of the agonistic elements as well as the sexual in relationships between the sexes, especially in the early stages. When pairs are formed, the hostile responses are gradually overcome; in such species copulation is not usually preceded by very elaborate displays. But when pairs are not formed and the two sexes meet only briefly for mating, the coordination between male and female necessary for successful copulation needs to be brought about in some other way. Hence the importance of the male's precisely ritualized display movements, to which the female responds with synchronized movements. Thus a highly coordinated mutual dance achieves in a few seconds what in a paired bird needs a prolonged period of mutual adjustment.

SUMMARY

The Black and White Manakin, *Manacus manacus*, a small, sexually dimorphic, mainly frugivorous passerine bird, was studied for 4½ years in an area of tropical forest in Trinidad.

There was an estimated adult population of some 500 birds in 450 acres of forest. It is considered that this density is considerably greater than is usual on the mainland of South America.

Males display at communal display grounds, where each bird clears a "court" on the forest floor. Each court has two or more saplings around its edges, which are used by the male in his display. Six display movements are described, and the accompanying mechanical sounds made by the specialized wing-feathers. Display goes on all through the day, with a marked peak soon after dawn and another peak in early afternoon.

Females visit the display grounds and join the males in a highly coordinated dance over the court. To mate, the male "slides down" one of the saplings onto the back of the female.

Observations on color-ringed birds showed that no pairs are formed. The males are polygamous and the females to a great extent promiscuous.

The communal display grounds result from the balanced social and aggressive tendencies of the male. There is keen competition for courts, and those near the center of the display ground are favored. Young males take many months to obtain a court.

Display continues all year, but is much reduced during the moult. The start of breeding varied in the five seasons by up to five months, but the season of moult did not vary appreciably.

The moult lasts for about 80 days for each bird. Juveniles moult into adult plumage in their second year, a little earlier than the adults.

The start of breeding is probably affected by food supply and weather, and its ending appeared to be correlated with the time of onset of the wet season.

The nest is attended by the female alone. The incubation period was 18-19 days, the fledging period 13-15 days. Only 19% of nests started produced fledged young. Females usually start 2-4 nests per season. Each female is estimated to rear on average one young per year.

Berry-bearing trees of the families Melastomaceae and Rubiaceae are of especial importance in the manakins' diet, producing a succession of fruit throughout the year. There was evidence of two periods of temporary food shortage. The breeding season coincides with the period of greatest availability of food.

The annual survival of adult males was 89%, and survival of females was also very high.

The evolution of communal displays is discussed.

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(In preparation) 2. The breeding seasons of Trinidad birds.

APPENDIX 1

The Display of Gould's Manakin

(*M. vitellinus*)

In March, 1958, the display of Gould's Manakin was studied on Barro Colorado Island and neighboring areas in Panama. Most of the observations were made at the display ground studied by Chapman in 1932 and 1935. As far as could be seen by field observations and by examination of motion picture film, its display was in general identical with that of *M. manacus*, with the following differences.

(1) "Fanning" was never seen, nor does Chapman mention it.

(2) The rolled snap, followed by "chee-poo," though the same as in *M. manacus*, appeared to be a more stereotyped and commoner display pattern. Chapman also remarked that it was a well-defined display.

(3) The "slide down the pole," following the "grunt-jump," was much more commonly performed by the individuals under observation than is normal in *M. manacus*. Twice a male was seen to slide down onto a female and copulate with her, after a preliminary dance similar to that of *M. manacus;* the sequence was filmed. Analysis of motion picture film shows that in one case, at the end of the slide, the bird remained head downward near the bottom of the perch for about a second, fanning its wings and vibrating its body somewhat as in the fanning display of *M. manacus*. The male that copulated also vibrated its body in the same way.

These observations provide a clue to the very puzzling "dirigible pose" described by Chapman. He described this display, which he saw performed by only one individual, as follows: "With bill touching the end of a slender, broken sapling the size of a pencil and about eighteen inches high, it fluttered its wings while holding a horizontal pose; then, with bill still pressed to the sapling, it slid down to the court and, with bill now touching a root, wings still fluttering, seemed to be standing on its head." Aerodynamically it is difficult to see how a manakin could flutter its wings and remain motionless in the air head downwards, since in such a position the force generated by its wings would have no down-

ward component. It seems almost certain that what Chapman saw was the "slide down the pole" (during which the bird's feet grip the perch, though this is not easy to see), followed by wing-fluttering at the bottom of the perch. In the poor light of the forest floor it is often difficult to see the details of these very rapid display movements.

(4) During low-intensity to-and-fro jumps across the court, without the initial snap and with normal whirring flight, a low "flup," clearly a wing noise, was often made on landing. The same sound was heard on two occasions when a bird landed after "snap-jumps," and was also occasionally heard made in mid-flight. It was never noted in *M. manacus*.

(5) Juvenile males, engaged in uncoordinated display behavior in the trees around the display ground, were several times seen to perform a display that was not recorded in *M. manacus*. Perched on a horizontal twig, the bird would look downwards, then with an initial little jump upward would jump down to a lower perch, uttering a weak plaintive "pu" on jumping. The same "pu" call was occasionally heard from juvenile males of *M. manacus* (p. 71), but it was not seen to be associated with a jump.

APPENDIX 2

Fruits Eaten by the Black and White Manakin

This list includes all the identified fruits found to be eaten by Black and White Manakins, by direct observation and by collection of regurgitated seeds from below nests, from display grounds, and in a few cases from trapped birds. The numbers following each plant name indicate the months in which the fruit was found to be eaten. These figures are used in Text-fig. 18, with the addition of the follow-

ing numbers of unidentified fruits in each month: January, 2; February, 5; March, 5; April, 16; May, 2; June, 4; July, 3; August, 1; September, 1; November, 3; December, 3.

I am much indebted to Mr. N. Y. Sandwith and Dr. J. J. Wurdack for help with many of these determinations.

Podocarpaceae	*Podocarpus* sp., 12
Gramineae	*Lasiacis sorghoidea* (Desr.) Hitchc. & Chase, 1
Araceae	*Monstera pertusa* (L.) de Vriese, 11
	Philodendron sp., 2
Liliaceae	*Smilax* sp., 4
Musaceae	*Heliconia* cf. *wagneriana* O. G. Peters, 11
	Heliconia hirsuta L.f., 4, 6
Zingiberaceae	*Costus spiralis* Rosc., 12
Marantaceae	*Stromanthe tonckat* (Aubl.) Eichl., 12
Moraceae	*Castilloa elastica* Cerv., 6, 7
	Cecropia peltata L., 6, 7, 9
	Ficus citrifolia Mill., 2
	Ficus clusiifolia Schott ex Spr., 2-7, 10, 11
Urticaceae	*Trema micrantha* (L.) Blume, 1, 5
Nyctaginaceae	*Pisonia eggersiana* Heimerl., 7, 8
	Pisonia sp., 7, 8
Lauraceae	*Ocotea canaliculata* (Rich.) Mez, 3-5
	Ocotea oblonga (Meissn.) Mez, 3, 5, 6
	Phoebe elongata (Vahl) Nees, 4, 5
Connaraceae	*Rourea surinamensis* Miq., 3-7, 11
Burseraceae	*Protium heptaphyllum* (Aubl.) March., 7, 8

Euphorbiaceae   *Alchornea triplinervia*   (Spr.) Müll. Arg., 12
                        Hieronyma caribaea   Urb., 6-8, 10, 11
                        Maprounea guianensis   Aubl., 11
                        Richeria grandis   Vahl, 3, 4

Aquifeliaceae   *Ilex* sp., 12
Sapindaceae   *Cupania rubiginosa*   (Poir.) Radlk., 3-5
                        Paullinia fuscescens   H. B. K., 10, 11
Tiliaceae   *Sloanea laurifolia*   (Bth.) Bth., 3
                        Sloanea stipitata   Spruce ex Bth., 5
Dilleniaceae   *Doliocarpus dentatus*   (Aubl.) Standl., 4-8
                        Pinzona calineoides   Eichl., 2-5
Flacourtiaceae   *Laetia procera*   (Poepp. & Endl.) Eichl., 2
Myrtaceae   *Myrcia leptoclada*   DC, 4, 5
Melastomaceae   *Clidemia* sp., 8, 12
                        Henriettea sp., 8
                        Miconia acinodendron   (L.) Sweet, 11
                        Miconia affinis   DC, 6-9
                        Miconia amplexans   (Crueg.) Cogn., 7
                        Miconia chrysophylla   (Rich.) Urb., 5
                        Miconia guianensis   (Aubl.) Cogn., 1, 2, 5-7, 12
                        Miconia kappleri   Naud., 11, 12
                        Miconia mucronata   (Desr.) Naud., 1, 2
                        Miconia multispicata   Naud., 1-6
                        Miconia myriantha   Benth., 10-12
                        Miconia nervosa   (Sm.) Tr., 5, 7
                        Miconia prasina   (Sw.) DC, 4-10
                        Miconia punctata   (Desr.) D. Don, 10-12
                        Miconia racemosa   (Aubl.) DC, 2
                        Miconia splendens   (Sw.) Griseb., 4
                        Miconia tomentosa   (Rich.) D. Don, 5, 6
Araliaceae   *Didymopanax morototoni*   (Aubl.) Dcne. & Planch., 1-3, 10-12
Boraginaceae   *Cordia bicolor*   A. DC, 7, 8
                        Cordia curassavica   (Jacq.) R. & S., 2, 4, 5, 12
Verbenaceae   *Aegiphila integrifolia*   (Jacq.) Jacks., 12
                        Lantana camara   L., 2, 5
Solanaceae   *Cestrum latifolium*   Lam., 2, 4, 5
Rubiaceae   *Amaioua corymbosa*   H. B. K., 2, 4-8
                        Cephaelis muscosa   (Jacq.) Sw., 1, 5, 6, 8
                        Cephaelis tomentosa   (Aubl.) Vahl, 2, 5, 6, 8, 9
                        Cephaelis sp., 1
                        Chiococca alba   (L.) Hitchc., 11, 12
                        Coussarea paniculata   (Vahl) Standl., 1
                        Gonzalagunia spicata   (Lam.) Gómez, 1, 12
                        Lacistema aggregatum   (Berg) Rusby, 5-7
                        Malanea macrophylla   Bartl., 2, 4
                        Palicourea crocea   (Sw.) DC, 1, 12
                        Psychotria cuspidata   (Bredem. ex Willd.), 4-6
                        Psychotria marginata   Sw., 4, 11, 12
                        Psychotria trinitensis   Urb., 4, 5, 11
                        Psychotria undulata, 2, 4, 6, 8-11
                        Rudgea freemanii   Sprague & Williams, 11
Compositae   *Wulffia baccata*   (L. fil.) Kze., 9

APPENDIX 3
WEIGHTS AND MEASUREMENTS
Weights

All trapped birds, unless they were wet, were placed in a cloth bag and weighed immediately after being caught. A spring balance, accurate to 0.5 gm., was used and was kept regularly calibrated. Altogether, 774 weights were obtained.

Eighteen birds were trapped and weighed more than once on the same day, two of them three times

and the remainder twice. Analysis of their weights showed that individuals increase their weight slightly in the course of the day, by approximately 0.75 gm. from 0700 to 1700 hours. For the analysis of seasonal weight-changes, weights taken from 1100 onwards need to be reduced by 0.5 gm. to make them comparable with those taken earlier. This has been done in the tables that follow. In the case of birds trapped more than once on the same day, the first weight has been used.

The mean of 185 weights of adult males was 18.20 gm. (range 15.5-22.5 gm.) The mean of 310 weights of females was 16.45 gm. (range 13.5-21.5 gm.). Juvenile males were intermediate, the mean of 59 weights being 17.02 gm. (range 13.5-19 gm.). (A considerable number of weights of birds in female plumage have not been used, as it was not known whether they were females or juvenile males.)

Seasonal changes in weight have been discussed in the body of the paper (p. 96).

Weights of adult males

gm.	Jan.-Feb.	Mar.-Apr.	May-Jun.	Jul.-Aug.	Sep.-Oct.	Nov.-Dec.
22.5				1		
22	1				1	
21.5	1					1
21			1	2		
20.5			2	2		
20	2		1	2	4	
19.5	1		1	1	1	5
19		5	4	4	4	2
18.5	5	5	9	4	5	4
18	4	4	10	6	4	5
17.5	2	4	11	4	2	6
17	4	1	5	5	6	2
16.5	6		5	1	1	4
16					1	
15.5						1

Weights of juvenile males

gm.	Jan.-Feb.	Mar.-Apr.	May-Jun.	Jul.-Aug.	Sep.-Oct.	Nov.-Dec.
19			3	3		
18.5		1		3	1	
18		1	1			
17.5		2	7			2
17		1	2	2	1	7
16.5			3		4	
16	4	1			2	
15.5	1		1	1		1
15		3				
14.5						
14						
13.5						1

Weights of females

gm.	Jan.-Feb.	Mar.-Apr.	May-Jun.	Jul.-Aug.	Sep.-Oct.	Nov.-Dec.
21.5			1			
21			2	1		
20.5			1			
20	1		1	2		
19.5			3			
19	2	2	5	1		1
18.5	1	2	6	2		1
18	1	1	6	2		
17.5	4	2	9	7	3	2
17	3	5	11	13	4	5
16.5	3	4	9	14	10	11
16	5	2	12	13	7	11
15.5	3	3	8	11	8	8
15	4	2	8	8	5	5
14.5	2	1	1	2	5	6
14	3			2		
13.5	1					

Measurements

The wings of nearly all the birds trapped were measured (the wing being held in the naturally closed position and not flattened). In addition the width of the outermost (10th) primary was measured 5 mm. from the tip in a smaller number of individuals, in order to find out if juvenile males are distinguishable from females by the degree of modification of the primaries (p. 70). The results, tabulated below, show that the wing-length of adult males averaged 2 mm. less than that of juvenile males and females, which did not differ appreciably from each other. Juvenile males, however, had slightly wider (less specialized) outer primaries than females.

Wing-lengths

mm.	Adult males	Juvenile males	Females
57		2	2
56		10	15
55	3	16	27
54	4	8	28
53	20	3	6
52	17	2	
51	11		

Width of outermost primary

mm.	Adult males	Juvenile males	Females
3.5		2	
3		9	13
2.5		3	14
2	17		3
1.5	5		

9

Longevity of Fishes in Captivity, as of September, 1956[1]

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FISHES are often credited with the attainment of tremendous age. Pliny, for example, attributed a normal life-span of 90 years to "Esox," probably the freshwater pike. Gesner, in his *Icones,* told of a pike 267 years old, and Baldinger (*ca.* 1802) mentioned one that died in its 277th year. It is well known that we can place little credence in figures such as these. As Frank Buckland wrote in 1880, "From the days of Gesner downwards, more lies—to put it in very plain language—have been told about the pike than any other fish in the world; and the greater the improbability of the story, the more particularly is it sure to be quoted" (Trautman & Hubbs, 1936). The skeleton of a supposedly 276-year-old pike, which had long resided in a museum, was found to consist of bones assembled from several individual fish (Breland, 1952), which, to say the least, throws doubt upon its authenticity. Furthermore, the abode of this pike had been a natural lake, in an area where this species is abundant, and it is not likely that positive identification of the same individual could have been made throughout the years. The same may be said of the various long-lived carp described by several authors (*e.g.* Suffield, 1874); it is probable that each of these records represents not a single fish, but a succession of individuals. Carp have been credited with life-spans ranging up to 375 years (Mehwald, 1872).

Nevertheless, figures for extreme longevity in fishes have been widely accepted, and they have helped to bring about the belief that fishes do not suffer senescence, but instead continue in the growing vigor of youth until their lives are cut short by accident (Brown, 1957). There is, of course, abundant evidence to the contrary.

Rasquin & Hafter (1951) and Gerking (1959), for example, showed that senility changes in at least some teleosts conform to the usual vertebrate pattern. Comfort (1956) discussed symptoms of "old age" in *Carassius auratus* and *Abramis brama.* Many small fishes, of the kinds usually kept in the home aquarium, become senile in a few months or years. Certain large fishes, on the other hand, such as the true halibuts (*Hippoglossus hippoglossus* and *H. stenolepis*), appear to reach an equilibrium in which they keep growing indefinitely at a low but nearly uniform increment *per annum* (Carl L. Hubbs, personal communication).

A number of techniques have been evolved by means of which the age of a fish may be determined, but most of these are applicable only to the first few years of life and have little value in the determination of the maximum age of a species. Length-frequency methods work very well until the age of maximum growth rate has passed, after which year classes are scarcely distinguishable. Counts of scale rings are accurate for a greater portion of the life span, but the rings tend to become obscured as the growth rate slows down. Gandolfi-Hornyold (1935) examined the scales of a European eel, *Anguilla anguilla,* that had lived for 24 years in the Aquarium at the Hydrobiological Institute of Toulouse; he could count only 11 growth rings. This discrepancy might be explained as the result of the specimen's having lived in a stable environment, without normal seasonal changes of temperature and food supply, but other observations indicate that eels may stop growing and stop forming growth marks on the scales. American eels, *Anguilla rostrata,* known to have been confined for a half-century in certain lakes of southern Michigan, were determined by Carl L. Hubbs, who was then Director of the Institute for Fisheries Re-

search at the University of Michigan, to be of normal adult size and to have only about 11 year marks on their scales (Hubbs, personal communciation). The scales of a European eel that lived in captivity for 57 years according to Macleod (1949), were apparently not studied.

The otolith method is more accurate than the scale method for some cases—especially when thin otolith sections are examined microscopically — but this method, too, is most useful in studying the important early growth years.

The method of direct observation, though fraught with inaccuracy, and limited severely in its applicability to animals under natural conditions, seems to be the least equivocal manner of determining the maximum age attained by fishes. A number of lists of such observations have been published, some of them setting forth the records of longevity as observed in a particular aquarium. Notable among these are the articles by Director Charles Haskins Townsend, Secretary Ida M. Mellen (1918) and Pathologist Ross F. Nigrelli, all of the New York Aquarium. Flower (1925, 1935) listed the records available to him; a few were the result of scale ring studies or other methods of estimating age, but the majority were based on direct observation. Some of the latter concern fishes that were observed in their natural environments, but most refer to aquarium specimens. Bourlière (1946) used Flower's data, plus a few additional figures, in a discussion of average age as compared to maximum age in 56 species of fishes.

In spite of these excellent lists, conversations and correspondence with aquarium curators led the author of the present paper to the realization that a number of unpublished records were in existence, and accordingly a program was undertaken to gather as many as possible for convenient reference. It is hoped that this list of records may be kept up to date, and revised at appropriate intervals—much in the manner of the annual list of records of snake longevity begun by Perkins (1947) and continued by Shaw (1958).

It was decided to limit records to those observations made in aquariums, excluding data from observations made in natural bodies of water, even though some of the latter are probably perfectly valid (see, for example, Gandolfi-Hornyold, 1935). It was also decided to exclude those species having a captive life span of less than five years. Information on the shorter-lived species would without doubt be extremely interesting, but its compilation would have been a tremendous task. Questionnaires were sent to 56 public aquariums in many parts of the world, requesting information on the longest-lived specimen of every fish known to have lived in captivity for five or more years. Nineteen replies were received, containing information on 238 species. To these have been added appropriate non-duplicated items from Flower (1925, 1935), Simpson (1957) and Nigrelli (1959).

The Aquarium of the Royal Zoological Society, Amsterdam, Holland, listed the largest number of species: 95. The same aquarium also reported the longest-lived fish—a sturgeon, *Acipenser ruthenus,* whose life span fell just four months short of 70 years.

There were more reports for cyprinids than for any other family—36 species in all. The oldest cyprinid is a carp, reported by the Frankfurt-am-Main Aquarium as having lived there for 38 years. Carp were listed by ten aquariums, more than for any other species, and the average maximum age was well over 19 years. Next most numerously represented is the Family Characidae, with 35 species. The oldest characin is a piranha, *Serrassalmus niger,* still living in Chicago's John G. Shedd Aquarium after 21 years and 4 months. Third is the Family Serranidae, with 25 or 26 species (one listing is simply *Epinephalus* sp.). The oldest individuals are the 30-year-old *Dicentrarchus labrax* of the Amsterdam Aquarium and several groupers of the genus *Epinephalus,* reported by A. W. C. Herre (in a letter to Earl S. Herald) as having lived in the Manila Aquarium for at least 30 years.

Several families are remarkable for the long lives of their members. Fifteen specimens of acipenserids are reported, for example, with an average captive life of 19 years and 6 months; this includes the figures for *Acipenser sturio,* which has apparently been relatively short-lived in captivity, with a record of less than 7 years. *Acipenser ruthenus,* on the other hand, was reported 6 times, and its captive life has averaged 31 years and 6 months.

The lepisosteids comprise another hardy group; the report lists 17 individuals, whose ages average 17 years and 7 months. The average captive life span of the 34 individuals of the Serranidae is 8 years and 10 months; only 6 of these, however, lived for longer than 10 years, and the median age of the records for the family lies between 7 and 8 years. This, incidentally, was one of the reasons for deciding upon the 5-year minimum for this report, instead of reducing the list by drawing the line at 10 years, as Perkins and Shaw have done with their snake records; a 10-year minimum would have resulted in the virtual exclusion of the serranids.

Muraenids have done well in captivity; 6 specimens of more than 20 years' residence were

reported by various aquariums. This does not compare favorably, however, with the legends telling of morays kept by Roman emperors through several generations. Perhaps such a long life presupposes a steady diet of Christians.

It will be noted that members of the family Esocidae are reported only three times and that the maximum age reported for any pike is only 10 years, the average being 8 years and 6 months. This makes it even more nearly certain that the old stories of bicentennarian pike are, to put it charitably, exaggerated.

It should be pointed out that some of the non-anadromous salmonids appear to be quite long-lived, and that there are hatchery records that far exceed the ones from aquariums listed here. For example, Leach (1924) states that female rainbow trout have been kept and regularly stripped for as long as 14 years, and there is a record of two lake trout that lived for 23 and 24 years in the Shasta hatchery operated by the California Division of Fish and Game (Anon., 1949).

Mullets (Mugilidae) are represented on the list by 5 species, one of which (*Liza chelo*) resided for 23 years in the aquarium of the Marine Biological Association of the United Kingdom in Plymouth. This was a surprise to the author, whose experience with the one species of *Mugil* occurring in southern California has been that it is a delicate fish, rarely living for more than a few months. California's single species of mullet is referred to the supposedly cosmopolitan *Mugil cephalus,* which is reported as having lived for 9 years in the aquarium at the Hellenic Hydrobiological Institute at the Station of Rhodes in the Dodecanese Islands. This difference may, of course, result from better equipment or better aquariological technique, or it may reflect some basic physiological difference between stocks from different regions.

Many fishes are known to adapt well to captivity, in that they show a low initial mortality after capture, but appear nonetheless to have a naturally short life expectancy. Aquarists find, for example, that as a rule most members of the family Blenniidae adapt easily to the conditions of captivity, and yet the family is represented on this list by a single report—a specimen of *Blennius pholis* that lived for 5 years in the Danmarks Akvarium in Charlottenlund, Denmark. Such regular aquarium inhabitants as the cyprinodonts, gobiids, clinids, and cottids are not reported at all, and it is tempting to infer that their natural life spans fall short of five years.

Also obviously absent from the list are most of the fast-moving pelagic fishes of many families, including the Coryphaenidae, Thunnidae, Istiophoridae and Xiphiidae. This is undoubtedly due, in some groups, to an inability to adapt to captivity, but in others—perhaps in most—it is again a question of a short span of life. Sailfish, for instance, very rarely reach the age of 5 years in the natural state (DeSylva, 1957), and F. G. Wood, Jr., of the Marine Studios, Marineland, Florida, has found that the life span of the dolphin (*Coryphaena hippurus*) may be even shorter (personal communication). Several investigators are finding the tunas to be short-lived.

Elasmobranch fishes are reported only 20 times. The oldest of these is a nurse shark (*Ginglymostoma*) reported as still living in the John G. Shedd Aquarium after 24 years.

The original request for information did not ask specifically for data concerning the manner of death, although this question will be included in future polls. Where such information was volunteered, it appeared that accident plays an important role even within the sheltered confines of a well-managed aquarium, and that every aquarist has suffered his share of catastrophes. Few of us, however, have had the misfortune to face wartime disasters such as those that brought about 100% fatalities in Munich, Bremerhaven and Manila. Douglas P. Wilson of Plymouth wrote that his old *Dicentrarchus labrax* died when vandals crept in through the aquarium's bomb-shattered windows and drained several of the tanks.

In the following list only the oldest record for each species is noted. The second column (A) shows the number of aquariums in which each species is reported to have lived for five or more years, while the third column (B) gives an abbreviation representing the home of the oldest listed individual. The last column (C) tells the age of this specimen in years and months; an asterisk (*) indicates that the specimen was still living when the report was first received by the author (in 1956). The sequence of families is that of Berg (1940).

scheme and to re-group synonymies. Unfortunately, circumstances beyond his control conspired to keep Dr. Hubbs from going over the list as thoroughly as would have been desirable, and any errors that remain must be attributed to the author.

ABBREVIATIONS

Abbreviations used in the Table below are as follows:

AMS—Aquarium of the Royal Zoological Society, Amsterdam, Holland.

BREM — Tiergrotten und Nordsee-Aquarium, Bremerhaven, Germany.

CHAR—Danmarks Akvarium, Charlottenlund, Denmark.

CHI—John G. Shedd Aquarium, Chicago, Illinois.

DAL—Dallas Aquarium, Dallas, Texas.

(F)—Following the abbreviation of an aquarium, refers to a report made by Flower (1925 or 1935).

FLOW — Refers to Flower (1925 or 1935), where the location of the specimen is not certain.

FRANK—Frankfurt-am-Main Zoological Garden, Frankfurt, Germany.

GIZ—Giza Zoological Gardens, Giza, Egypt.

HERM — Ocean Aquarium, Hermosa Beach, California.

LON—The London Aquarium, London, England.

MON—Institut Océanographique, Monaco.

MUN — Tierpark Hellabrunn, Munich, Germany.

NY — New York Aquarium, New York, New York.

NZ — Wellington Aquarium, Wellington, New Zealand.

PHIL—Fairmount Park Aquarium, Philadelphia, Pennsylvania.

PLY — Marine Biological Association of the United Kingdom, Plymouth Laboratories, Plymouth, England.

RHO—Athens Academy, Hellenic Hydrobiological Institute, Station of Rhodes, Dodecanese Islands, Greece.

SF—Steinhart Aquarium, San Francisco, California.

SIO—T. Wayland Vaughan Aquarium-Museum, Scripps Institution of Oceanography, University of California, San Diego.

SHA—Shasta Trout Hatchery, Mt. Shasta, California.

TOL—Toledo Zoo Aquarium, Toledo, Ohio.

WUP — Zoologischer Garten, Wuppertal, Germany.

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956
(Limited to reported life of five years or more.)

Column A—Number of aquariums reporting given species.

Column B—Aquarium reporting the oldest specimen.

Column C—Age of the oldest specimen (years/months).

     * Indicates that the specimen was living as of September, 1956.

FAMILY AND SPECIES	A	B	C
HETERODONTIDAE—Horned Sharks			
Heterodontus francisci (Girard)	1	SIO	12/3
OROLECTOLOBIDAE—Nurse Sharks			
Ginglymostoma cirratum (Bonnaterre)	1	CHI	24*
CARCHARIIDAE—Sand Sharks			
Carcharias taurus Rafinesque	2	NY	9
SCYLLIORHINIDAE—Cat Sharks			
Scylliorhinus canicula (Linnaeus)	4	LON(F)	8/4
S. stellaris (Linnaeus)	2	AMS	19/4
TRIAKIDAE—Smooth Dogfishes			
Triakis semifasciata Girard	1	HERM	6
PRISTIDAE—Sawfishes			
Pristis pectinatus Latham	1	CHI	8/1
RAJIDAE—Skates			
Raja clavata Linnaeus	4	CHAR	14/7
R. maculata Montagu	1	LON(F)	5/7
R. punctata Risso	1	RHO	6/10

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
(Limited to reported life of five years or more.)

FAMILY AND SPECIES	A	B	C
DASYATIDAE—Stingrays			
Dasyatis pastinaca (Linnaeus)	2	LON(F)	21
TORPEDINIDAE—Electric Rays			
Torpedo marmorata (Linnaeus)	1	RHO	6/10
CERATODONTIDAE—Australian Lungfish			
Neoceratodus forsteri (Günther)	3	CHI	22/4*
LEPIDOSIRENIDAE—South American Lungfish			
Lepidosiren paradoxus Fitzinger	1	AMS	9/8
PROTOPTERIDAE—African Lungfishes			
Protopterus aethiopicus Heckel	2	LON(F)	6/10
P. annectens Owen	4	NY	23*
P. dolloi Boulenger	1	LON(F)	8/8
POLYPTERIDAE—Bichirs			
Polypterus senegalis Cuvier	1	GIZ(F)	34
ACIPENSERIDAE—Sturgeons			
Acipenser brevirostrum Le Sueur	1	NY	7
A. fulvescens Rafinesque	3	CHI	23/3
A. ruthenus Linnaeus	6	AMS	69/8
A. sturio Linnaeus	4	AMS	9/11
Scaphyrhynchus platorhynchus (Rafinesque)	1	DAL	13*
POLYODONTIDAE—Paddlefishes			
Polyodon spathula (Walbaum)	1	CHI	5/2
AMIIDAE—Bowfins			
Amia calva Linnaeus	3	NY	30
LEPISOSTEIDAE—Gars			
Lepisosteus osseus (Linnaeus)	6	NY	30
L. platostomus Rafinesque	5	NY	20
L. productus (Cope)	1	TOL	8/3
L. spatula Lacépède	5	CHI	23/4*
MEGALOPIDAE—Tarpons			
Tarpon atlanticus (Valenciennes)	2	CHI	19/10*
SALMONIDAE—Trouts			
Coregonus clupeaformis (Mitchill)	2	NY	12
Hucho hucho (Linnaeus)	1	MUN	10
Salmo gairdnerii Richardson	1	NY	5
S. trutta fario Linnaeus	1	NY	5
S. trutta lacustris Linnaeus	1	LON(F)	10/4
Salvelinus fontinalis (Mitchill)	1	NY	5
S. malma (Walbaum)	1	SHA	19
ESOCIDAE—Pikes			
Esox lucius Linnaeus	2	LON(F)	10
E. masquinongy Mitchill	1	NY	10
NOTOPTERIDAE—Notopterids			
Notopterus notopterus (Pallas)	1	AMS	9/4
OSTEOGLOSSIDAE—Osteoglossids			
Osteoglossum bicirrhosum Vandelli	1	CHI	6/3
PANTODONTIDAE—Pantodon			
Pantodon bucholzi Peters	2	AMS	6/9
MORMYRIDAE—Mormyrids			
Marcusenius isidori Valenciennes	1	FLOW	28/11
Mormyrus kannume Forskål	1	CHAR	16/3
CHARACIDAE—Characins			
Astyanax bimaculatus (Linnaeus)	1	AMS	18
A. fasciatus mexicanus (Filippi)	1	LON(F)	6/9
Chalceus macrolepidotus Cuvier	2	MUN	19*
Colossoma nigripinnis (Cope)	1	MUN	6*
Copeina guttata (Steindachner)	1	AMS	6/6
Corynopoma riisei Gill	1	AMS	13
Ctenobrycon spilurus (Valenciennes)	2	AMS	14/7
Exodon paradoxus Müller & Troschel	1	CHAR	6/8

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
(Limited to reported life of five years or more.)

FAMILY AND SPECIES	A	B	C
Gymnocorymbus ternetzi (Boulenger)	2	AMS	8/2
Hemigrammus caudovittatus Ahl	1	AMS	12/2
H. ocellifer (Steindachner)	1	NZ	5
H. uniliniatus Gill	1	LON(F)	5/2
Hemiodus semitaeniatus Kner	2	CHI	16/1
Hepsetus odeo (Bloch)	1	MUN	6*
Hyphessobrycon bifasciatus Ellis	1	AMS	9
Leporinus fasciatus (Bloch)	3	MUN	18
L. friderici Bloch	3	MUN	18
L. megalepis Günther	2	CHAR	18/1
Metynnis maculatus (Kner)	1	LON(F)	11/11
M. roosevelti Eigenmann	3	MUN	17/6*
M. schreitmuelleri Ahl	1	WUP	6/4*
Moenkhausia oligolepis (Günther)	1	AMS	14/6
Myleus asterias (Müller & Troschel)	3	MUN	18*
M. gurupyensis Steindachner	1	MUN	18*
M. schomburgkii (Jardine)	1	MUN	18*
Mylossoma duriventre (Cuvier)	2	MUN	18*
Nannaethiops unitaeniatus Günther	1	AMS	6/2
Pristella riddlei (Meek)	1	AMS	9/2
Prochilodus insignis Schomburgk	2	WUP	6/10*
Serrasalmus nattereri (Kner)	2	MUN	17
Serrasalmus niger (Schomburgk)	1	CHI	21/4*
S. rhombeus (Linnaeus)	1	TOL	19
S. spilopleura Kner	1	CHAR	7/9
Thoracocharax stellatus (Kner)	1	CHAR	9/5
ELECTROPHORIDAE—Electric Eel			
Electrophorus electricus (Linnaeus)	3	AMS	12/1
CATOSTOMIDAE—Suckers			
Ictiobus bubalus (Rafinesque)	1	TOL	16/4
Ictiobus cyprinella (Valenciennes)	1	TOL	16/4
CYPRINIDAE—Minnows			
Abramis brana (Linnaeus)	2	AMS	15/9
Aphyocypris pooni Lin	1	AMS	7/8
Balantocheilus melanopterus Bleeker	1	AMS	11/11
Blicca bjoerkna (Linnaeus)	1	AMS	16/10
Brachydanio albolineatus (Blyth)	1	AMS	7/6
B. nigrofasciatus (Day)	1	AMS	7/1
B. rerio (Hamilton-Buchanan)	1	AMS	8
Carassius auratus (Linnaeus)	7	NY	10
Cyclocheilichthys apogon (Valenciennes)	1	AMS	6/2
Cyprinus carpio Linnaeus	10	FRANK	38
Danio malabaricus (Jerdon)	1	AMS	7/10
Epalzeorhynchus kalopterus (Bleeker)	1	CHAR	12
Leuciscus cephalus (Linnaeus)	2	AMS	7
L. idus (Linnaeus)	3	AMS	21/7
Notemigonus crysoleucas crysoleucas (Mitchill)	1	NY	7
Osteocheilus hasseltii (Valenciennes)	1	MUN	18
O. vittatus (Valenciennes)	1	MUN	6
Puntius chola (Hamilton-Buchanan)	1	AMS	11/4
P. cumingi (Günther)	1	AMS	6/5
P. dunkeri (Ahl)	1	MUN	11
P. everetti (Boulenger)	2	MUN	11
P. lateristriga (Valenciennes)	2	AMS	18/5
P. nigrofasciatus (Günther)	1	AMS	7
P. oligolepis (Bleeker)	1	AMS	8/1
P. schwanfeldi (Bleeker)	1	AMS	11/3
P. semifasciolatus (Günther)	1	AMS	18/8
P. ticto (Hamilton-Buchanan)	1	AMS	12/10
P. titteya Deraniyagala	1	AMS	6/7

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
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FAMILY AND SPECIES	A	B	C
Rasbora einthovenii (Bleeker)	1	AMS	10/11
R. heteromorpha Duncker	2	LON(F)	6/9
R. trilineata Steindachner	1	AMS	6/10
Rhodeus sericeus (Pallas)	2	AMS	10
Rhinichthys atratulus atratulus (Hermann)	1	NY	5
Rutilus rutilus (Linnaeus)	1	AMS	9/3
Scardinius erythrophthalmus (Linnaeus)	5	CHI	20/3*
Tinca tinca (Linnaeus)	1	CHAR	7/11
COBITIDAE—Loaches			
Botia hymenophysa (Bleeker)	1	AMS	6
Cobitis taenia Linnaeus	2	FLOW	10/1
Nemacheilus barbatulus (Linnaeus)	1	AMS	8/3
ARIIDAE—Sea Catfishes			
Galeichthys felis (Linnaeus)	2	PHIL	15/3*
DORADIDAE—Doradid Catfishes			
Doras sp.	1	AMS	26/5
SILURIDAE—Sheatfishes			
Silurus glanis Linnaeus	3	CHAR	11/6
ICTALURIDAE—North American Catfishes			
Ictalurus nebulosus (Le Sueur)	1	AMS	13/6
I. punctatus (Rafinesque)	2	TOL	8/5
Pylodictis olivaris (Rafinesque)	2	TOL	16/1
CHACIDAE—Chacid Catfishes			
Chaca chaca (Hamilton-Buchanan)	1	AMS	6/4
SACCOBRANCHIDAE—Airbreathing Catfish			
Saccobranchus fossilis (Bloch)	4	AMS	12/11
CLARIIDAE—Clariid Catfishes			
Clarius batrachus Valenciennes	2	AMS	13/2
SYNODONTIDAE—Upside-down Catfishes			
Synodontis schal (Bloch & Schneider)	2	FLOW	31
MALAPTERURIDAE—Electric Catfish			
Malapterurus electricus (Linnaeus)	5	CHI	8/1
PIMELODIDAE—South American Catfishes			
Phractocephalus hemeliotropus (Bloch & Schneider)	1	CHI	12/2
Pimelodella gracilis (Valenciennes)	2	AMS	11/11
Pimelodus clarias (Bloch)	1	AMS	27/1
Rhamdia sebae (Valenciennes)	2	AMS	30/8
CALLICHTHYIDAE—Mailed Catfishes			
Corydoras aeneus Gill	2	MUN	12
C. julii Steindachner	1	WUP	6/5
LORICARIIDAE—Armored Catfishes			
Loricaria microlepidogaster Regan	1	AMS	7/7
Plecostomus commersonii (Valenciennes)	3	MUN	19/7
P. punctatus (Valenciennes)	2	MUN	18
P. rachovii Regan	1	MUN	18
ANGUILLIDAE—Freshwater Eels			
Anguilla anguilla (Linnaeus)	6	MUN	19
A. rostrata (Le Sueur)	2	DAL	17*
MURAENIDAE—Morays			
Gymnothorax funebris Ranzani	2	CHI	20/4*
G. mordax Ayres	3	SIO	26
Muraena clepsydra Gilbert	1	SIO	6*
M. helma Linnaeus	4	AMS	20/3
CONGRIDAE—Congers			
Conger conger (Linnaeus)	2	RHO	9*
GADIDAE—Cods			
Lota lota lacustris (Walbaum)	1	NY	5
Pollachius pollachius (Linnaeus)	1	PLY	5
CYPRINODONTIDAE—Killifishes			
Aplocheilus lineatus (Valenciennes)	1	AMS	7/7

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
(Limited to reported life of five years or more.)

FAMILY AND SPECIES	A	B	C
Epiplatys chaperi (Sauvage)	1	AMS	9/10
POECILIIDAE—Livebearers			
Limia nigrofasciata (Regan)	1	AMS	5/7
ZEIDAE—Dories			
Zeus faber Linnaeus	1	PLY	5
MUGILIDAE—Mullets			
Liza auratus Risso	1	RHO	9
L. capito Cuvier	2	AMS	14
L. chelo Cuvier	2	PLY	23
Mugil cephalus Linnaeus	2	RHO	9
M. rammelsbergii Tschudi	1	AMS	14
ATHERINIDAE—Silversides			
Melanotaenia maccullochi Ogilby	1	AMS	7/7
M. nigrans (Richardson)	1	AMS	17/7
CHANNIDAE—Snakeheads			
Channa striata Bloch	1	AMS	5/10
Ophicephalus obscurus Günther	1	CHAR	11/7
LATIDAE—Nile Perches			
Lates niloticus (Gmelin)	1	FLOW	12
SERRANIDAE—Basses			
Centropristis striatus (Linnaeus)	1	PHIL	5
Dicentrarchus labrax (Linnaeus)	4	AMS	30
Epinephalus aeneus (Geoffroy)	1	RHO	8/5*
E. adscensionis (Osbeck)	1	PHIL	6/11
E. analogus Gill	1	SIO	5*
E. chrysotaenia Doderlein	1	RHO	8/4
E. gigas (Brünnich)	2	MON	29/2
E. guaza (Lacépède)	1	RHO	9/1*
E. guttatus (Linnaeus)	3	PHIL	14/10*
E. itajara (Lichtenstein)	1	NY	12
E. labriformis (Jenyns)	1	SIO	5*
E. morio (Valenciennes)	1	NY	7
E. sp.	1	MON	7/1
E. striatus (Bloch)	3	PHIL	9/1
E. summana Forskål	1	CHAR	8
Morone americana (Gmelin)	1	NY	7
Mycteroperca bonaci (Poey)	1	PHIL	7/11
M. tigris (Valenciennes)	1	NY	5
M. venenosa (Linnaeus)	1	NY	5
Paralabrax clathratus (Girard)	2	SIO	12
P. maculatofasciatus (Steindachner)	1	SIO	8*
P. nebulifer (Girard)	1	SIO	8*
Roccus chrysops (Rafinesque)	1	DAL	6
R. saxatilis (Walbaum)	3	NY	24
Serranus cabrilla (Linnaeus)	1	RHO	7/5
S. scriba (Linnaeus)	1	RHO	7/5
THERAPONIDAE—Theraponids			
Therapon jarbua (Forskål)	1	LON(F)	7/7
KUHLIIDAE—Kuhliids			
Kuhlia taeniura (Cuvier)	1	AMS	8/9
K. sandvicensis (Steindachner)	1	SF	7*
CENTRARCHIDAE—Sunfishes			
Ambloplites rupestris rupestris (Rafinesque)	2	NY	18
Centrarchus macropterus (Lacépède)	2	AMS	16/9
Enneacanthus chaetodon (Baird)	1	AMS	7/1
E. gloriosus (Holbrook)	1	AMS	11
Lepomis gibbosus (Linnaeus)	3	AMS	16
L. megalotis (Rafinesque)	1	LON(F)	6/4
Micropterus dolomieui Lacépède	2	NY	11
M. salmoides salmoides (Lacépède)	3	TOL	13/5

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
(Limited to reported life of five years or more.)

FAMILY AND SPECIES	A	B	C
Pomoxis nigromaculatus (Le Sueur)	1	NY	12
PERCIDAE—Perches			
Perca flavescens (Mitchill)	1	NY	12
P. fluviatilis Linnaeus	2	LON(F)	10/8
Stizostedion lucioperca (Linnaeus)	2	LON(F)	9/1
CARANGIDAE—Jacks			
Caranx crysos (Mitchill)	1	PHIL	5/11
C. hippos (Linnaeus)	1	NY	5
Selene vomer (Linnaeus)	1	NY	5
LUTJANIDAE—Snappers			
Lutjanus jocu (Bloch & Schneider)	2	NY	14/7
L. griseus (Linnaeus)	1	NY	7
L. synagris (Linnaeus)	1	NY	7
L. argentiventris (Peters)	1	SF	11*
POMADASYIDAE—Grunts			
Anisotremus davidsonii (Steindachner)	2	SF	9*
Haemulon sciurus (Shaw)	1	NY	5
Orthopristis chrysopterus (Linnaeus)	1	PHIL	5/6
SCIAENIDAE—Croakers			
Aplodonotus grunniens Rafinesque	1	TOL	16/5
Corvina nigra (Bloch)	1	MON	11/11
Cynoscion regalis (Bloch & Schneider)	1	NY	5
C. xanthulus Jordan & Gilbert	1	SIO	5/2
Micropogon undulatus Linnaeus	1	PHIL	6/2
Pogonias cromis (Linnaeus)	2	PHIL	10/9
Roncador stearnsi (Steindachner)	2	HERM	6
Umbrina roncador Jordan & Gilbert	2	SF	6
Sciaenops ocellata (Linnaeus)	2	PHIL	12/1
SPARIDAE—Porgies			
Archosargus probatocephalus (Walbaum)	1	NY	6
Dentex dentex (Linnaeus)	2	RHO	8
Diplodus annularis (Linnaeus)	2	RHO	9
D. sargus (Linnaeus)	2	RHO	9
Oblada melanura (Linnaeus)	1	RHO	9
Pagellus centrodontus (de la Roche)	1	PLY	7
P. mormyrus (Linnaeus)	1	RHO	9
P. pagrus (Linnaeus)	2	RHO	7
Puntazzo puntazzo (Cetti)	1	RHO	9
Sparus auratus Linnaeus	2	RHO	8
Spondyliosoma cantharus (Linnaeus)	3	MON	8
MONODACTYLIDAE—Monodactylids			
Monodactylus argenteus (Linnaeus)	2	MUN	5/6
TOXOTIDAE—Archerfishes			
Toxotes jaculatrix (Pallas)	2	SF	6/5*
SCORPIDAE—Halfmoons			
Medialuna californiensis (Steindachner)	1	HERM	6
GIRELLIDAE—Nibblers			
Girella nigricans (Ayres)	2	HERM	7
EPHIPPIDAE—Spadefishes			
Chaetodipterus faber (Broussonet)	1	NY	5
Platax orbicularis (Forskål)	2	MON	7
P. teira (Forskål)	1	AMS	6/5
SCATOPHAGIDAE—Scats			
Scatophagus argus (Linnaeus)	3	CHAR	9/3
CHAETODONTIDAE—Butterflyfishes			
Holacanthus isabelita (Jordan & Rutter)	1	NY	5
NANDIDAE—Nandids			
Badis badis (Buchanan-Hamilton)	1	AMS	7/6
Pristolepis grooti (Bleeker)	1	AMS	8/1

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
(Limited to reported life of five years or more.)

FAMILY AND SPECIES	A	B	C.
CICHLIDAE—Cichlids			
Astronotus ocellatus (Cuvier)	4	WUP	17/3
Aequidens pulcher (Gill)	1	AMS	5/3
Cichlasoma bimaculatum (Linnaeus)	1	AMS	11/10*
C. biocellatum Regan	1	AMS	6/10
C. facetum (Jenyns)	1	AMS	10/4
C. hellabrunni Ladiges	2	WUP	9/4
C. maculicauda Regan	1	AMS	8/11
C. nigrofasciatum (Günther)	1	LON(F)	9
C. severum (Heckel)	3	AMS	10/8
Hemichromis bimaculatus Gill	1	AMS	14/6
Herichthys cyanoguttatus carpintis (Jordan & Snyder)	1	LON(F)	5/6
Pterophyllum eimekei Ahl	2	AMS	5/4
Symphysodon discus Heckel	1	WUP	5/4*
Tilapia macrocephala (Bleeker)	1	AMS	8/6
T. mossambica (Peters)	1	NY	6
T. natalensis (Weber)	1	AMS	12/7
T. nilotica (Linnaeus)	1	AMS	11/11
T. zilli (Gervais)	1	CHAR	5/1
POMACENTRIDAE—Damselfishes			
Amphiprion ephippium (Bloch)	1	CHAR	16/6
Chromis chromis (Linnaeus)	1	RHO	6/6
Dascyllus aruanus (Linnaeus)	1	CHAR	5/11
Hypsipops rubicunda (Girard)	1	SIO	7
Premnas biaculeatus (Bloch)	1	CHAR	8/11
LABRIDAE—Wrasses			
Coris julis (Linnaeus)	1	RHO	7
Pimelometopon pulchrum (Ayres)	3	SF	23
Labrus bergylta Ascanius	1	PLY	5
L. festivus Risso	1	RHO	8
Tautoga onitis (Linnaeus)	2	NY	8
SCARIDAE—Parrotfishes			
Scarus cretensis (Bloch)	1	RHO	7
BLENNIIDAE—Blennies			
Blennius pholis Linnaeus	1	CHAR	5
SIGANIDAE—Siganids			
Siganus chrysospilos (Bleeker)	1	AMS	7/5
ANABANTIDAE—Climbing Perches			
Anabas testudineus (Bloch)	5	DAL	16
Belontia signata (Günther)	2	LON(F)	10/7
Colisa lalia Hamilton-Buchanan	1	AMS	6/11
Ctenops vittatus (Valenciennes)	1	AMS	6/11
Osphrenemus goramy Lacépède	1	AMS	8/11
Polyacanthus hasselti Valenciennes	1	AMS	10/10
Trichogaster leerii (Bleeker)	1	AMS	5/8
ELEOTRIDAE—Sleepers			
Dormitator maculatus (Bloch)	1	AMS	14/2
Eleotris vittata Duméril	1	CHAR	11/10
Oxyeleotris marmorata (Bleeker)	1	AMS	20/5*
SCORPAENIDAE—Scorpionfishes			
Pterois volitans (Linnaeus)	1	MON	10/4
Scorpaena guttata guttata Girard	1	SIO	10
S. porcus Linnaeus	2	RHO	9
S. scrofa Linnaeus	1	RHO	8
TRIGLIDAE—Gurnards			
Trigla lucerna Linnaeus	3	LON(F)	6/9
SCOPHTHALMIDAE—Turbots			
Psetta maxima (Linnaeus)	2	AMS	10/1
BOTHIDAE—Lefteyed Flounders			
Zeugopterus punctatus (Bloch)	1	CHAR	5/5

LONGEVITY OF FISHES IN CAPTIVITY AS OF SEPTEMBER, 1956 (Continued)
(Limited to reported life of five years or more)

FAMILY AND SPECIES	A	B	C.
PLEURONECTIDAE—Righteyed Flounders			
Platichthys flesus (Linnaeus)	1	RHO	5/2
SOLEIDAE—Soles			
Solea solea (Linnaeus)	2	RHO	5/5
MASTACEMBELIDAE—Mastacembelids			
Mastacembelus erythrotaenia Bleeker	1	AMS	10/11
Rhynchobdella aculeata (Bloch)	1	AMS	9
BALISTIDAE—Triggerfishes			
Balistes capriscus Gmelin	4	RHO	9
B. vetula Linnaeus	1	PHIL	5/1
LAGOCEPHALIDAE—Puffers			
Arothron reticularis (Bloch & Schneider)	1	MON	7/1
TETRAODONTIDAE—Puffers			
Amblyrhynchotes honckenii (Bloch)	1	LON(F)	5/5
Tetraodon lineatus (Linnaeus)	2	CHAR	9/3
T. fluviatilis (Hamilton-Buchanan)	3	CHAR	9/3
CANTHIGASTERIDAE—Puffers			
Canthigaster margaritatus Rüppell	1	LON(F)	6/11
DIODONTIDAE—Porcupinefishes			
Diodon hystrix (Linnaeus)	1	PHIL	7/4
BATRACHOIDIDAE—Toadfishes			
Opsanus tau (Linnaeus)	3	CHI	13/11

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10

Hybridization Experiments in Acheilognathine Fishes (Cyprinidae, Teleostei). A Comparison of the Intergeneric Hybrids between *Tanakia tanago* and *Rhodeus spinalis* and *Rhodeus ocellatus* from Korea and Japan

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(Plates I & II; Text-figure 1)

IN a recent paper the present author (Duyvené de Wit, in press) has summarized the results of his investigations into the presence of gametic compatibility between a number of acheilognathine[1] species.

From Text-fig. 1, in which the ability of these species to cross is represented diagramatically, it appears that gametic compatibility is not limited to the subspecific and specific levels, but also manifests itself on the generic level. In the majority of the intergeneric crosses, the F_1 offspring consisted of phenotypical males only, but the intergeneric hybrids between the allopatric species *Tanakia tanago* (Tanaka) from Japan and *Acheilognathus himantegus* (Günther) from Taiwan consisted of fertile males and females. These fishes were allowed to interbreed freely in the presence of freshwater mussels and this experimental interbreeding population has now been carried through its fourth generation. The phenotypic character of all four generations has remained stable.

In another paper (Duyvené de Wit, 1961), we have expressed the view that *Rhodeus spinalis* (Oshima) from Taiwan and the two strains of *Rhodeus ocellatus* (Kner), which have their habitats in Japan and Korea respectively, represent three allopatric geographic subspecies belonging to a single species. As will be seen from Text-fig. 1, the hybrids produced from these strains consisted of fertile males and females.

When comparing the phenotypes of these three strains, slight differences between both the Korean and the Japanese varieties of *R. ocellatus* are apparent, while the Taiwan species, *R. spinalis*, is fairly similar to both strains of *R. ocellatus*. In order to investigate whether the genomes of the three supposed subspecies would express themselves differently in the F_1 generations when crossed with a single species of bitterling belonging to another genus, we mated them with the Japanese species *Tanakia tanago*. In Table 1, the six possible breeding combinations have been designated 1 to 6.

TABLE 1.

	T. tanago ♀	*T. tanago* ♂
R. ocellatus (Japan) ♀		1
R. ocellatus (Japan) ♂	2	
R. ocellatus (Korea) ♀		3
R. ocellatus (Korea) ♂	4	
R. spinalis (Taiwan) ♀		5
R. spinalis (Taiwan) ♂	6	

MATERIAL AND METHOD

All crossings were performed by means of artificial insemination. The number of larvae produced by the six crosses ranged from 8 to 20, but some died in the course of development as a result of infectious diseases. The following results are based on the hybrids that reached the adult stage.

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[1]Following Chu (1935) and Hubbs & Kuronuma (1943), the designation Acheilognathinae instead of Rhodeinae is used, because *Acheilognathus* (Bleeker, 1863) has priority over *Rhodeus* (Günther, 1868).
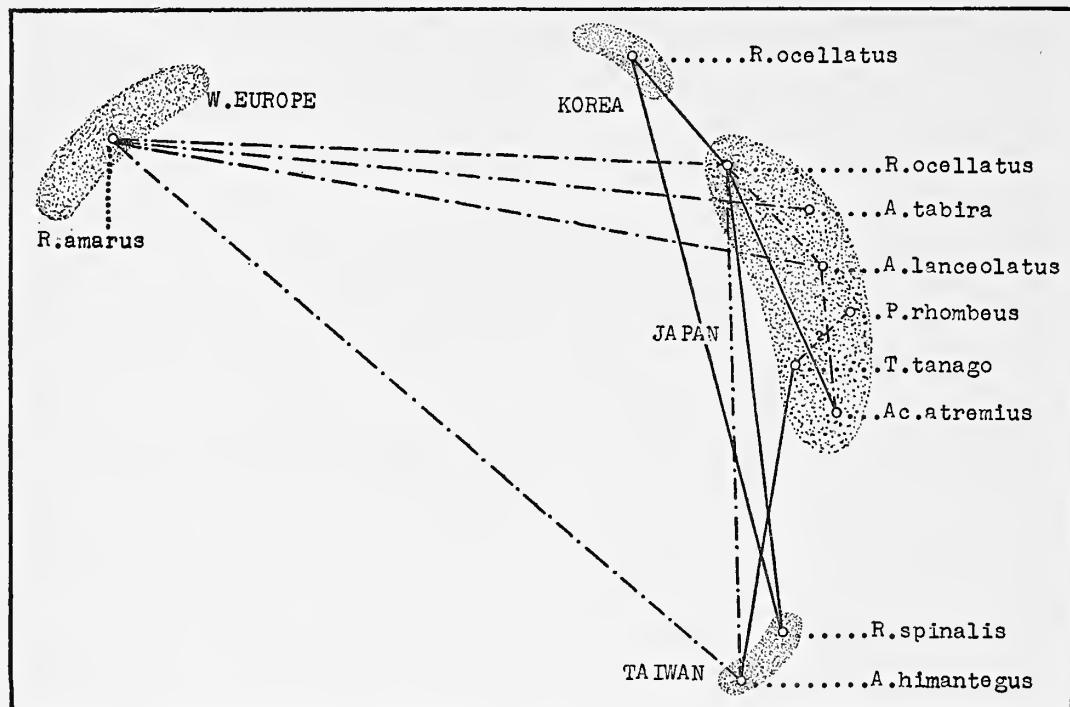
Text-fig. 1. Diagram showing the gametic affinities between a number of acheilognathine species from W. Europe, Korea, Japan and Taiwan, on the subspecies, species and generic levels, according to Duyvené de Wit [in press].

RESULTS

1. *R. ocellatus* (Japan) ♀ × *Tanakia tanago* ♂

This combination yielded eight hybrids of different body size and shape. Two of them were large and fairly similar to the maternal species, *R. ocellatus* (Japan), four were small and showed greater similarity to the paternal species, *T. tanago,* while two were intermediate. All hybrids showed a male phenotype. During the spawning season they displayed full nuptial colors. Tubercles were present on the top of the snout. No milt production could be detected by stripping, however.

Representative specimens from the large and the small form of hybrid are illustrated in Figs. 3 and 4 respectively. The maternal species, *R. ocellatus* from Japan, is illustrated in Fig. 1 and the paternal species, *T. tanago*, in Fig. 2.

2. *T. tanago* ♀ × *R. ocellatus* (Japan) ♂

From this, the reciprocal combination, five hybrids were obtained. They also were not uniform in appearance. Three of them were large and in body size and shape tended to resemble the paternal species, *R. ocellatus* (Japan). The remaining two hybrids were medium-sized. One of them tended to resemble the maternal species,

T. tanago, while the other was more similar to the paternal species, *R. ocellatus* (Japan). All hybrids showed a male phenotype. Nuptial colors and tubercles on top of the snout were present during the spawning season, but no milt could be obtained by stripping.

One of the large hybrids is illustrated in Fig. 7. A specimen of the maternal species, *T. tanago,* is illustrated in Fig. 5, and one of the paternal species, *R. ocellatus* from Japan, in Fig. 6.

It should be noted that the hybrids of the reciprocal combinations are different in general appearance.

3. *R. ocellatus* (Korea) ♀ × *T. tanago* ♂

From this combination six hybrids were obtained. They were relatively small and fairly uniform in size and body shape. In general appearance and with respect to their small size they were much more similar to the paternal species, *T. tanakia,* than to the maternal species, *R. ocellatus* (Korea). All hybrids showed a male phenotype. During the spawing season they displayed bright nuptial colors and tubercles were present on the top of the snout. Milt production could not be detected by means of stripping.

A representative hybrid specimen is illustrated

in Fig. 9. The maternal species, *R. ocellatus* from Korea, is illustrated in Fig. 8.

4. *T. tanago* ♀ × *R. ocellatus* (Korea) ♂

From this cross five hybrids were obtained. Four of them were fairly large. With respect to body size and shape they tended to resemble the paternal species, *R. ocellatus* (Korea). One of these showed a coin-like body shape, an abnormality that is also sometimes encountered in the pure-bred strain of *R. ocellatus*. The remaining hybrid was much smaller than its brood mates. All hybrids showed a male phenotype. They displayed full nuptial colors during the spawning season and tubercles were present on the top of the snout. No milt production could be detected by stripping.

A representative hybrid specimen is illustrated in Fig. 11. The paternal species, *R. ocellatus* from Korea, is illustrated in Fig. 10.

In their general appearance the hybrids of the combinations 3 and 4 differ considerably from each other.

5. *R. spinalis* ♂ × *T. tanago* ♀

From this combination fourteen hybrids were obtained. With respect to body size they showed a gradual transition from large to very small. The largest specimens tended to resemble the maternal species, although the dorsal part of the body was less curved than in *R. spinalis*. The smaller ones were more similar to the paternal species, *T. tanago*. Except the three smallest specimens, which probably were neuters, the hybrids showed a male phenotype. During the spawning season they displayed full nuptial colors, and tubercles were present on the top of the snout. No milt could be obtained by stripping.

Representative specimens of the large and the small hybrids are illustrated in Fig. 13. The maternal species, *R. spinalis*, is illustrated in Fig. 12.

6. *T. tanago* ♀ × *R. spinalis* ♂

From this combination, five hybrids were obtained. They were fairly uniform in size and body shape and tended to resemble the paternal species in that the dorsal part of the body was curved as in *R. spinalis*. All of them showed a male phenotype. During the spawning season they displayed full nuptial colors. Tubercles were present on the top of the snout, but milt could not be obtained by stripping.

A representative specimen of the present hybrids is illustrated in Fig. 15. The paternal species, *R. spinalis*, is illustrated in Fig. 14.

The hybrids of combinations 5 and 6 show considerable difference in general appearance.

DISCUSSION

The question whether the genomes of the three supposed geographical subspecies of *R. ocellatus* under investigation express themselves differently in the six kinds of hybrids that could be produced by crossing them with a single test species, *T. tanago*, must be answered in the affirmative.

In their general appearance the hybrids of the combinations 1 + 2, 3 + 4 and 5 + 6 appeared to differ considerably from one another. Moreover, the hybrids obtained from three hybrid combinations (1, 3 and 5) were different from their respective reciprocal ones (2, 4 and 6). Finally, the six separate F_1 generations showed no uniformity among their brood mates. These findings are in sharp contrast to the fact that the progenies obtained from *R. ocellatus* (Japan) × *R. ocellatus* (Korea), *R. ocellatus* (Japan) × *R. spinalis* (Taiwan) and *R. ocellatus* (Korea) × *R. spinalis* (Taiwan) were largely uniform in body form and size.

On the other hand, all present hybrid generations correspond in showing the male phenotype, by displaying nuptial colors during the spawning season and in the absence of milt production.

The lack of uniformity in the six F_1 generations probably points to incomplete genetic compatibility and presents an interesting problem for future karyological research.

The taxonomic status of the six kinds of hybrids under discussion here will be published separately.

SUMMARY

1. Intergeneric hybrids have been obtained from the combinations *Rhodeus ocellatus* (Japanese strain) × *Tanakia tanago*, *Rhodeus ocellatus* (Korean strain) × *Tanakia tanago* and *Rhodeus spinalis* × *Tanakia tanago*.

2. All hybrids showed the male phenotype. During the spawning season they displayed full nuptial colors, but milt production could not be detected by means of stripping.

3. The six kinds of hybrids obtained from the three combinations and their reciprocals differed considerably from one another, and the variability among the individuals of the separate F_1 generations was conspicuous. This is interpreted as an expression of incomplete genetic compatibility between the respective male and female gametes.

ACKNOWLEDGEMENTS

to Prof. Moon-ki Chyung and Mr. Kyun Hyun Kim for supplying the Korean acheilognathine species, to Professor Fah-hsuen for supplying the Taiwan acheilognathine species, to Mr. F. G. de Jardin and Mr. R. A. Cragg for providing photographs of the illustrated specimens, and to Mr. C. A. van Ee for the drawing of the diagram. The financial assistance of the Board of the University of the Orange Free State and of the Council for Scientific and Industrial Research of the Republic of South Africa is gratefully acknowledged.

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[In press] Hybridization experiments in acheilognathine fishes (Cyprinidae, Teleostei). The hybrids between female *Acheilognathus lanceolatus* and *Rhodeus amarus,* and male *Acheilognathus himantegus.* Can. J. Zool.

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EXPLANATION OF THE PLATES

Plate I

Fig. 1. Female specimen of *Rhodeus ocellatus* from Japan. Standard length 44 mm.

Fig. 2. Male specimen of *Tanakia tanago.* Standard length 42 mm.

Fig. 3. Specimen of a large hybrid obtained from the combination female *Rhodeus ocellatus* (Japan) × male *Tanakia tanago.* Standard length 61 mm.

Fig. 4. Specimen of a small hybrid obtained from the combination as indicated in the legend of Fig. 3. Standard length 37 mm.

Fig. 5. Female specimen of *Tanakia tanago.* Standard length 35 mm.

Fig. 6. Male specimen of *Rhodeus ocellatus* from Japan. Standard length 69 mm.

Fig. 7. Specimen of a hybrid obtained from the combination female *Tanakia tanago* × male *Rhodeus ocellatus* (Japan). Standard length 60 mm.

Fig. 8. Female specimen of *Rhodeus ocellatus* from Korea. Standard length 44 mm.

Fig. 9. Specimen of a hybrid obtained from the combination female *Rhodeus ocellatus* (Korea) × male *Tanakia tanago.* Standard length 37 mm.

Plate II

Fig. 10. Male specimen of *Rhodeus ocellatus* from Korea. Standard length 61 mm.

Fig. 11. Specimen of a hybrid obtained from the combination female *Tanakia tanago* × male *Rhodeus ocellatus* (Korea). Standard length 51 mm.

Fig. 12. Female specimen of *Rhodeus spinalis.* Standard length 39 mm.

Fig. 13. Specimen of a large hybrid obtained from the combination female *Rhodeus spinalis* × male *Tanakia tanago.* Standard length 54 mm. Left corner: specimen of the very small hybrid form. Standard length 25 mm.

Fig. 14. Male specimen of *Rhodeus spinalis.* Standard length 46 mm.

Fig. 15. Specimen of a hybrid obtained from the combination female *Tanakia tanago* × male *Rhodeus spinalis.* Standard length 45 mm.

FIG. 1

FIG. 2

FIG. 3

FIG. 4
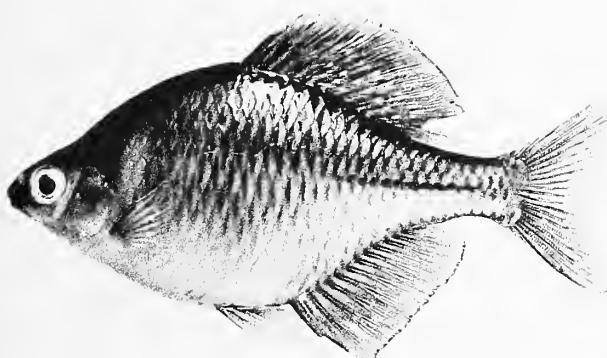
FIG. 5

FIG. 6
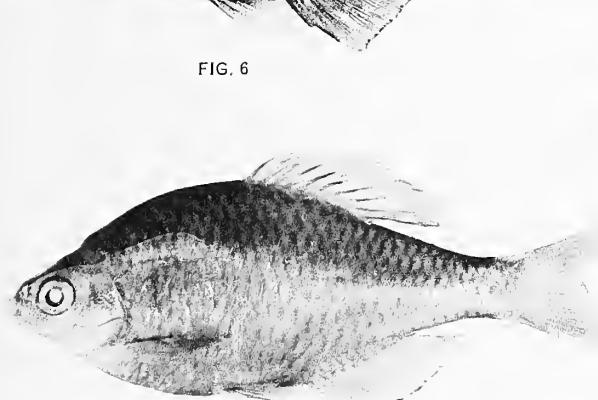
FIG. 7

FIG. 8

FIG. 9

INTERGENERIC HYBRIDS BETWEEN TANAKIA TANAGO AND RHODEUS SPINALIS
AND RHODEUS OCELIATUS FROM KOREA AND JAPAN

PLATE II
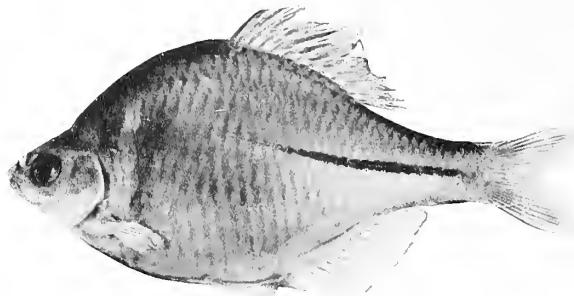
FIG. 10

FIG. 11

FIG. 12

FIG. 13

FIG. 14

FIG. 13

FIG. 15

INTERGENERIC HYBRIDS BETWEEN TANAKIA TANAGO AND RHODEUS SPINALIS
AND RHODEUS OCELIATUS FROM KOREA AND JAPAN

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE

NEW YORK ZOOLOGICAL SOCIETY

Contents

11

Observations of the Sound Production Capabilities of the Bottlenose Porpoise: A Study of Whistles and Clicks[1]

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(Plates I-IV; Text-figures 1-6)

INTRODUCTION

FOR centuries man has been aware that of all the creatures of the sea the whales and porpoises are among the most vociferous. Recent research (Norris *et al.*, 1961; Kellogg, 1958; Kellogg, *et al.*, 1953) has demonstrated that one functional aspect of this vocal behavior is its use in navigation and food-finding by the process of echo-location. This form of behavior has proved to be particularly interesting to laymen and the military as well as psychologists and zoologists, and it is not surprising that the other vocalizations produced by these animals have been relatively neglected. That they have the ability to emit several sounds in addition to those used for echo-location raises the possibility that other functions, *e.g.* communication, are involved.

The best known cetacean is the Atlantic bottlenose porpoise, *Tursiops truncatus* (Montagu), but before a total and accurate description of the complex acoustic behavior displayed by this species can be drafted, a great many more data are needed. At present, information is available on the frequency range, duration and directionality of the signals it uses for echo-location. Some aspects of the swimming behavior associated with this activity have also been described (Norris *et al.*, 1961). On the other hand, little is known about the mechanisms used by the porpoise to produce its wide array of vocal signals, and the range and variability of the animal's

non-echo-location acoustic output has not been specified.

This paper describes some preliminary efforts to investigate the sound production apparatus and signal repertoire of the Atlantic bottlenose porpoise. The animals and facilities were made available through the cooperation of Marineland of the Pacific, where all observations were made.

We would like to express our gratitude to Mr. Wm. F. Monahan, Marineland of the Pacific, to Dr. John Dreher and Mr. William Sutherland, Lockheed Aircraft, and to Dr. Carl George, American University, Beirut, Lebanon, for their able assistance. We also wish to thank Mrs. Muriel Johnson for help in the preparation of the manuscript.

COLLECTION OF PORPOISE VOCALIZATION DATA

To initiate this investigation it was necessary to acquire an adequate sample of the vocal behavior of *Tursiops*. This was achieved by recording the sound production of a group of five to eight specimens which were confined in a concrete holding tank, 30 feet in diameter and 5 feet deep. Recordings from a single animal confined in a plastic-lined holding tank, 30 feet in diameter and 4 feet deep, were also obtained. In all, some six hours of taped data were collected during several recording sessions. A block diagram of the instrumentation used is presented in Text-fig. 1. The over-all response of this recording system was from 100 cps to 17 kcps, plus or minus two decibels, and the sensitivity was down less than 12 db at 20 kcps, with a tape speed of 7½ inches per second. The equivalent
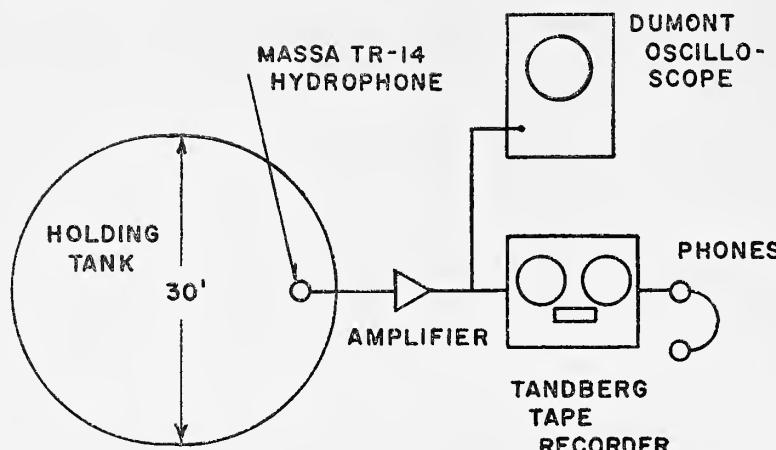
TEXT-FIG. 1. Block diagram showing instrumentation used to record porpoise vocalizations.

frequency response of the system at the reduced playback speed used for analysis, which was 3.75 inches per second, did not suffer, but was approximately one decibel better than that of the recording system.

The system used for the data analysis consisted of the tape recorder and a Sona-Graph sound spectrograph (Kay Electric Co., Pinebrook, N. J.). This instrument analyzes a complex signal as a function of time and frequency. The resultant portrayal, known as a sonagram, displays frequency along the vertical axis, time along the horizontal axis and intensity by the darkness of the pattern. The use of this type of equipment for the analysis of biological sounds has been thoroughly reviewed in Lanyon & Tavolga (1960).

Analyses of the recorded data indicated that all of the sounds produced by the animals fell into one of the following three categories.

(a) Clicks or plosive sounds—echo-location pulses with a time duration of .001 to .01 second and a frequency range 100 cps to 35 kcps and beyond. Although the recording equipment used in these studies has an upper frequency response limit of 20-24 kcps, it is adequate for studying certain aspects of the echo-location clicks. The echo-location signal may have its greatest intensity in the 20-35 kcps range; however, it appears in several regions of frequency reinforcement with considerable energy from 3 kcps to 20 kcps, which is within our recording range. We were thus able to determine and track pulse rate, frequency shift and other physical data of the echo-location clicks by utilizing the portions of the signal of lower frequency (below 22 kcps).

(b) Whistles—frequency modulated signals, very narrow band with one or two overtones; frequency range 4,000 to 20,000 cps.

(c) Barks—sounds rich in overtones which must be produced in a system of complex resonators, frequency range 200 to 16,000 cps. Sonagrams showing a frequency *versus* time display for each of these types of sound emissions are presented in Plate I.

Sounds associated with echo-ranging were the most frequently observed acoustic phenomena. The animals were constantly echo-ranging the tank, checking for possible environmental change, *e.g.*, the addition of food. Repetition rates of this type of signal varied from one or two pulses per second to rates as high as 525 pulses per second.

The next most frequently observed sounds were whistles. These whistles were usually associated with movement of one or more animals about the tank. The lowest frequency observed was 3.7 kcps and the highest about 20-22 kcps, with the signal durations varying from .10 to 3.6 seconds. The shape of the whistle contours were quite variable. In all, a total of 18 basically different whistles were observed. Stylized frequency *vs.* time plots of some of the most frequently observed whistles are presented in Text-fig. 2.

Barks were the most infrequently observed sound. The fundamental frequency of these signals varied between 200 and 300 cps with harmonics as high as 16 kcps. Signal duration was usually about 0.10 second. These barks usually occurred when the animals were engaged in some stationary activity rather than swimming.

MECHANISMS FOR SOUND PRODUCTION

Anatomical examination of the nasal and laryngeal tracts of the delphinids *Tursiops truncatus* and *Stenella graffmani* reveals structures that appear to be suited for the production of each of the sounds previously mentioned.

For the production of clicks (plosive echo-
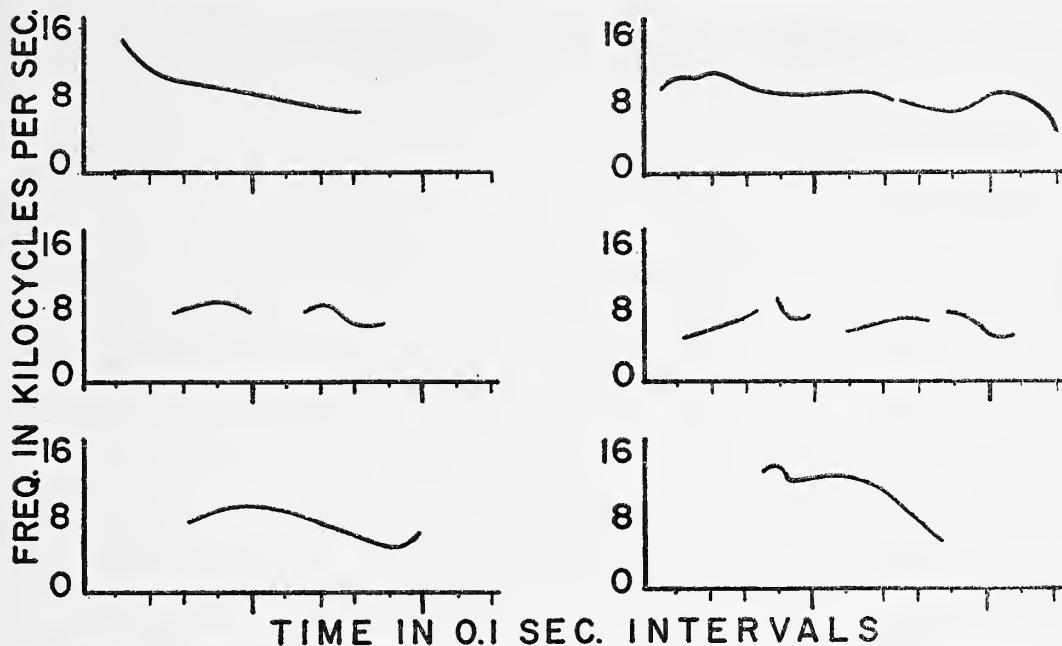
TEXT-FIG. 2. Composite diagrams showing frequency *vs.* time plots of six of the most frequently occurring whistles produced by *Tursiops truncatus.*

location sounds), the complex nasal sac system described by Lawrence & Schevill (1956) appears to be the most likely source. This system represents an interconnecting pneumatic tract with several *cul de sacs,* valves and lips.

The nasal sacs comprise the distal part of the nasal airway and lie within the soft tissues of the head, dorsad of the bony nares and premaxillary bones of the skull (Text-fig. 3). They are located slightly below the fatty and connective tissue of the melon, or forehead, surrounded by their own muscle groups. All of them are paired. The premaxillary sacs are the largest and lie immediately on top of the smooth premaxillary bones, immediately anterior to the distal openings of the bony nares. The premaxillary sacs
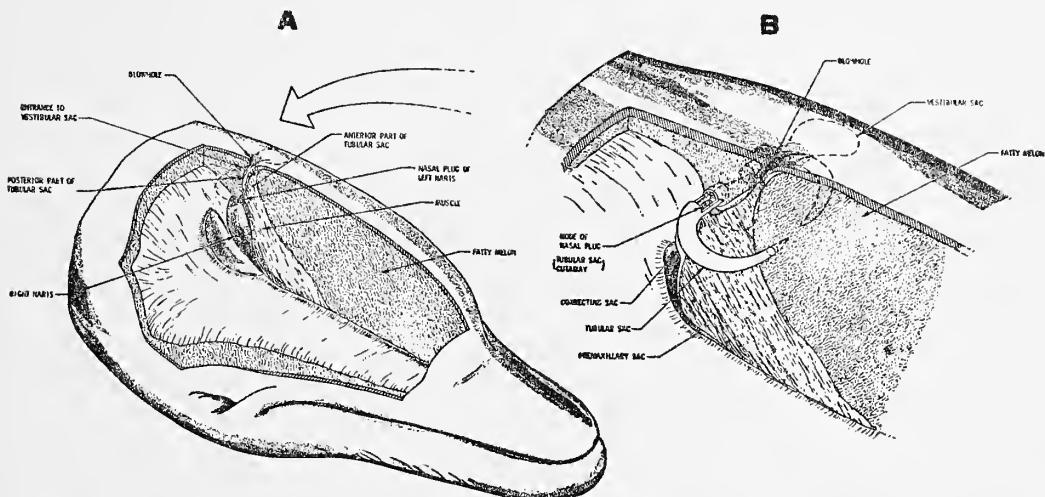
TEXT-FIG. 3. Sketch of a bottlenose porpoise head with a cut-away exposing the naso-laryngeal tract, indicating the approximate locations of the nasal sacs, fatty melon and bony nares. **A.** Cutaway of whole head. **B.** Expanded view of sac system.

communicate with the bony nares, their soft posterior wall continuing as an extension to become the nasal plugs. The vestibular sacs are the outermost pair and lie posterolateral to, and just below, the lips of the blowhole. As Lawrence & Schevill (1956) have pointed out, "There is a considerable mass of tissue lying between the vestibular area and the dorsal surface of the plugs and it is here that the last two pairs of sacs, the tubular and the connecting, lie embedded. These are both true sacs in the sense that they are distinct from the main air passage and connect with it only via rather small, well marked openings." The tubular sacs are U-shaped with a slit opening in the lateral portion connecting to the main airway. They lie nearly horizontal in the head, almost surrounding the main airway. The connecting sacs are appendices to the tubular sacs and provide the only direct passageway for air from the tubular into the premaxillary sacs and then the main airway. These connections are along the distal edges of the nasal plugs near the base where the premaxillary sacs join the airway and open into the bony nares. Near the top part of the nasal plugs, at a point opposite the slit openings of the tubular sacs, there are small tongue-like nodes. Each of these appendages is inserted into the opening of the tubular sac (Text-fig.3). The intrinsic muscles appear to function as mechanisms to distend the tubular sacs, and transverse ligaments beneath the posterior limbs of the tubular sacs help stiffen the posterior walls of the passage (Lawrence & Schevill, 1956). These interconnections and other structures provide a passage for communication between the main air passages and the tubular sac. Such an arrangement links these sacs with the nasal airway without disturbing the position of the nasal plug and breaking the water- and gas-tight seal of the blowhole. It seems from examination of the musculature, the surrounding connective tissue and the lips of the tubular sacs that these mechanisms are capable either of maintaining or accepting the air pressures necessary to generate high frequency echo-location clicks. When air flows past the nodes of the nasal plugs projecting into the tubular sac, these nodes could vibrate, acting as a type of "raspberry" generator. This arrangement is not unlike the human tongue, inserted between the lips, used in producing a "Bronx cheer."

If the lens-shaped fatty body, or melon, characteristically found in the "forehead" of toothed whales could function as a variable focus "acoustic lens," then the complex nasal sacs and the accompanying pneumatic valve system would be ideally positioned. In light of Reysenbach de Haan's (1956) observations that blubber and fatty tissue are essentially acoustically transparent due to their excellent impedence match for water, this arrangement would allow little energy loss of the air-produced sounds when transmitted into the water. Further evidence for this system exists in the somewhat modified asymmetric parabolic reflector formed by the dense bone of the premaxillae. Thus an acoustic lens, the melon, backed-up with the specially modified skull, could act to "focus" the animal's echo-location signals. The observations that when completing echo-location searches, in order to find targets or pick up food, *Tursiops* bends its head in a rapid circular scanning motion and appears to point its melon in the direction of search indicate that the sound pulse used is generated in the nasal sac system (Kellogg, 1960). Norris *et al.* (1961) noticed that a blindfolded *Tursiops* had difficulty in echo-locating objects positioned on a line below the melon.

Although the literature suggests that the Odontoceti have no vocal cords, as they exist in man for example, their larynx is a complex structure. The larynges of *Tursiops* and *Stenella* are shown in Plate II. Structurally, these larynges differ from those of terrestrial mammals in the elongated arytenoid cartilages and the accompanying epiglottic cartilage which form the aryteno-epiglottid tube. From the standpoint of structure alone, this smooth-surfaced, hard backed and constricted tube does form an ideal sound generator. For almost one hundred years investigators have speculated how the toothed whales could use this unique larynx to produce sound (Murie, 1871, and Turner, 1868). Vibration of the tissue folds and of the elongated arytenoid cartilages have both been considered. To the best of our knowledge, however, experimental data either to support or refute these hypotheses have never been published.

SOUND SIMULATION TESTS

A series of experiments using the excised larynx and two severed heads of *Stenella* and the head of a fresh specimen of *Tursiops* was carried out. The basic plan was to deliver a controlled flow of air at various pressures through the larynx and the heads to determine whether sound could be produced, and if so, to analyze its characteristics and measure the pattern with which it was radiated from the head. A block diagram of the instrumentation used during these tests is presented in Text-fig. 4.

To test the excised larynx of *Stenella*, a glass connector was inserted into the trachea and air delivered through it at a pressure of 1 to 2 psi and a flow of 10 to 15 liters per minute. The lips of the arytenoids were approximated by manipulation with forceps. This procedure re-
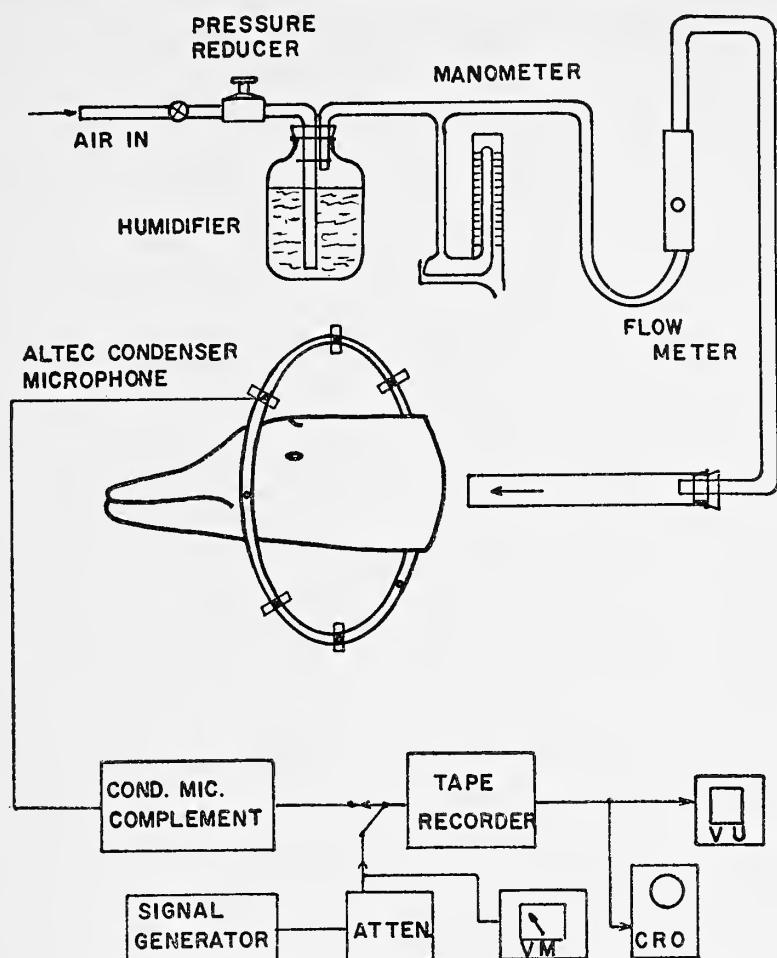
TEXT-FIG. 4. Block diagram of the instrumentation used for the sound simulation tests.

sulted in the production of a wide range of sounds depending on the amount of pressure applied and the proximity of the lips to each other.

Tests with the whole head required the same instrumentation as those with the excised larynx. To permit free access around the heads, they were suspended from a cross-arm with a glass connector inserted into the trachea. In this series of tests, no manipulation was used except to make certain that the aryteno-epiglottid tube of the larynx was well seated in the ventral openings of the bony nares. Sound was produced at pressures and flow rates of the same order of magnitude as those in the previous test with the larynx alone.

The sounds produced during both types of test were quite similar. Depending on the pressure applied and position of the larynx, sounds ranging from barks, rich in harmonics, to whistles were produced (Plate III, A & B). In addition to these sounds, short duration pulse-type signals (Plate III, C), very similar to those employed in echo-location, were generated by air flowing through the nasal sac system of one specimen of *Stenella*. As air was forced into the excised heads, the blowhole became closed and the pressure was allowed to build up to two pounds per square inch. With the blowhole effectively sealed, the air sacs, especially the vestibular ones, would become inflated. Pressures inside the sacs, vestibular and premaxillary, were checked by inserting a spinal tap needle through the tissues into the sac. The core of the needle was then removed and a manometer attached. In the case of sounds similar to echo-location clicks, it was necessary for the sacs to be filled with air before any clicks were heard. If pressure was applied to the melon, for example by a hand pressed across the forehead, the sacs could be collapsed. Although the exact mechan-

Stenella Graffmani MLP 60-11 ♀ 69
Ref: OASPL 93db re: .0002 dynes/cm² (0 db)
0.25 in. from head
Airflow: 10 liters/min
1.04 lb/in²

TEXT-FIG. 5. Over-all sound pressure levels measured at various locations .25 inches from the head of a specimen of *Stenella graffmani* during sound simulation tests.

whales (Odontoceti) noted by anatomists. Hosokawa (1950) has reported this in the musculature of the larynx of the sperm whale; Lawrence & Schevill (1956) have noticed this in the nasal sac system and skulls of *Tursiops truncatus* and *Stenella plagiodon;* and we have found that the nasal sacs in *Tursiops truncatus* and *Stenella graffmani* are larger on the right side. In fact, all the delphinids examined by the junior author have exhibited an asymmetrical development of the cranium and nasal sac system. These include *Delphinus bairdi, Tursiops gilli, Lagenorhynchus obliquidens, Stennella longirostus* and *Globicephala scammoni*.

The indirect evidence presented so far indicates that porpoises do have structures that can produce a variety of different types of sounds. It does not, however, add any support to the contention that echo-location clicks and whistling sounds are produced by separate mechanisms. The following observations, however, add credence to the supposition of specialized sound producers.

All of the initial observations of sound production using specimens of *Tursiops* were accomplished with groups of five or more animals. In order to simplify the sound analyses and observations on behavior, one animal was transferred to the smaller plastic-lined tank one day before testing. In this tank the porpoise was not restrained and was given food immediately. Using the previously described equipment, recorded *Tursiops* sounds, whistles and clicks were broadcast into the tank. Until this test, not a great deal of success had been achieved in eliciting whistles from solitary animals. During this test and for a period after stimulation, however, several long whistles were produced by the animal. The most interesting aspect of this behavior was that in all cases, the solitary animal produced echo-location signals and whistles simultaneously. Lilly & Miller (1961) report similar behavior from a physically restrained, solitary *Tursiops*. The time duration of the whistle portion of the simultaneous emissions that they observed ranged from .1 to .4 seconds. We have observed whistle durations from .45 to 1.5 seconds, the majority of them being longer than .6 second. Several sonagrams of these simultaneous signals are shown in Plate IV in which it can be seen that the whistles are overlaid on the pulsed signal. The whistles are not highly modulated and appear normal, that is, as they do in Plate I, B. If only one mechanism for sound production was involved, the whistle could be expected to show some of the modulations of the echo-location signal.

ism that produced these signals was not determined, deflation of the upper or distal nasal tract stopped the echo-location clicks. These sounds were achieved with air pressures of 1 psi within the specimens of *Stenella* and 1.5 psi within the *Tursiops*. Air flow was 10 liters per minute for both.

In addition to the sonagraphic analyses made of the clicks produced with the heads, measurements were also made of the over-all sound pressure level ¼ of an inch and 15 inches from the head at every 60° in the horizontal and vertical planes. The measures of over-all sound pressure level near the surface of the head at both distances are shown by the polar plots presented in Text-figs. 5 & 6. Most noteworthy is the asymmetrical radiation, with the stronger signal output on the right. This asymmetry immediately calls to mind the general asymmetry of cranial structures in toothed

TEXT-FIG. 6. Over-all sound pressure levels measured every 60°, 15 inches from the head of a specimen of *Stenella graffmani* in both **A** vertical plane and **B** horizontal planes.

CONCLUSIONS AND SUMMARY

1. All of the natural vocalizations of a group of *Tursiops* and a single individual *Tursiops* can be placed in one of the three following categories: Plosive or pulse signals, whistles and barks.

2. Both *Tursiops truncatus* and *Stennella graffmani* have anatomical structures capable of producing a variety of sounds under conditions of artificial stimulation. These sounds are not unlike the ones produced naturally by these animals. Sounds artificially produced in the head of a specimen of *Stenella* showed an asymmetrical sound radiation pattern corresponding with the asymmetry of the cranial structures.

3. *Tursiops* is capable of producing echo-location pulses and whistles simultaneously.

4. Anatomical and behavioral evidence, as well as sound pressure measurements, indicate that the echo-location clicks are produced in the nasal-sac system of porpoises. Within the sac-system, the tubular sacs combined with the nasal plug nodes appear to be the site of sound production. It is only through the tubular and connecting sacs that we find a continuous air passage, the vestibular and pre-maxillary sacs being *cul de sacs*.

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EXPLANATION OF THE PLATES

Plate I

Fig. 1. Sonagrams of examples of the three types of sound produced underwater by *Tursiops truncatus*. **A.** Clicks or pulses. **B.** Whistle. **C.** Bark.

Plate II

Fig. 2. **A.** Larynx from *Stenella graffmani*. **B.** Larynx from *Tursiops truncatus*.

Plate III

Fig. 3. **A.** Sonagrams of sound produced by passing air through the excised larynx of *Stenella graffmani*. **B.** Sonagrams of sound produced by passing air through a severed head from *Stenella graffmani*. **C.** Sonagram of short-duration, repetitive, pulse sounds generated by air flow through the nasal sac system of one specimen of *Stenella graffmani*.

Plate IV

Fig. 4. Sonagrams of four instances of simultaneous production of echo-location pulses and whistles by a single isolated *Tursiops truncatus*.
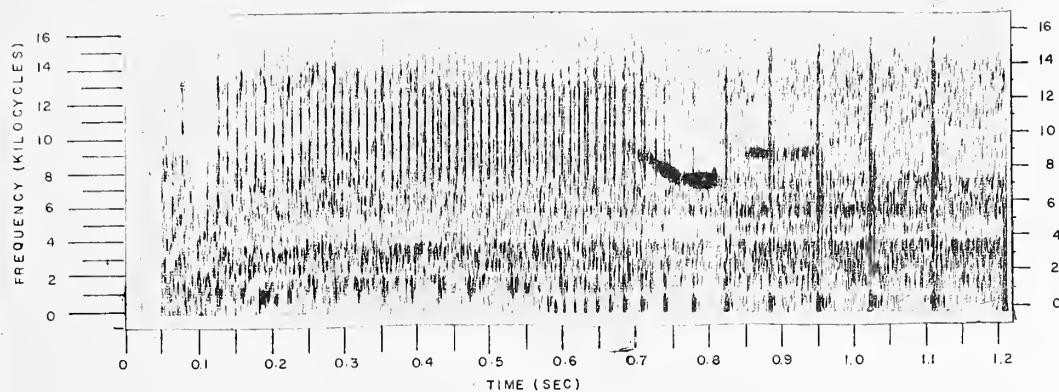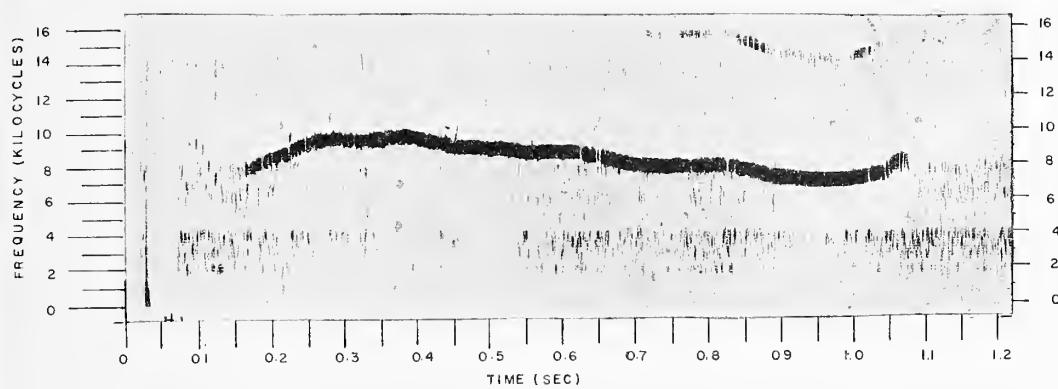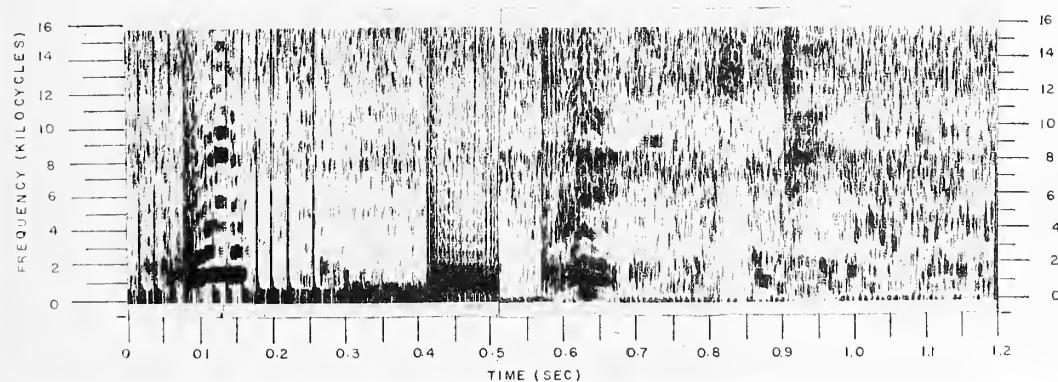
PLATE I

OBSERVATIONS OF THE SOUND PRODUCTION CAPABILITIES OF THE
BOTTLENOSE PORPOISE: A STUDY OF WHISTLES AND CLICKS

TRACHEA
ARYTENOID CARTILAGES
ADDITUS LARYNGIS
EPIGLOTTIS
THYROID CARTILAGE

A

B
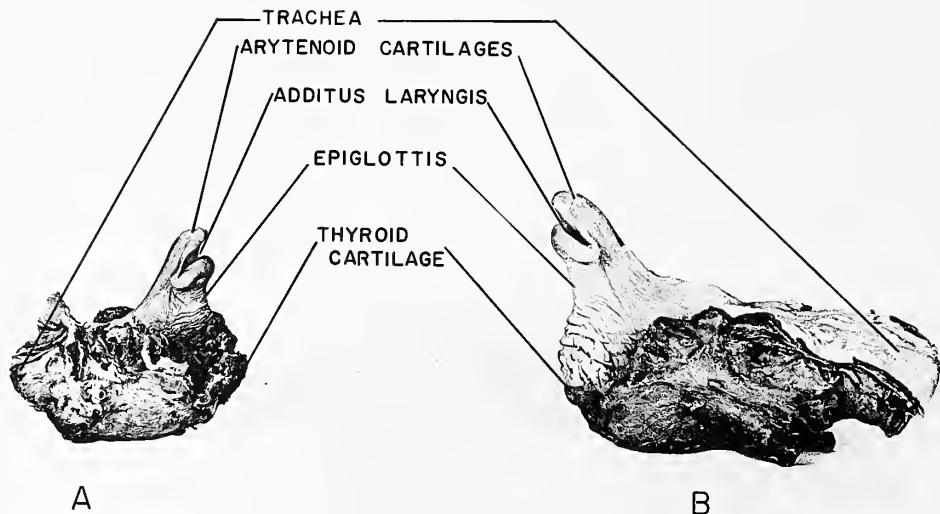
EXCISED LARYNX FROM
STENELLA GRAFFMANI

EXCISED LARYNX FROM
TURSIOPS TRUNCATUS
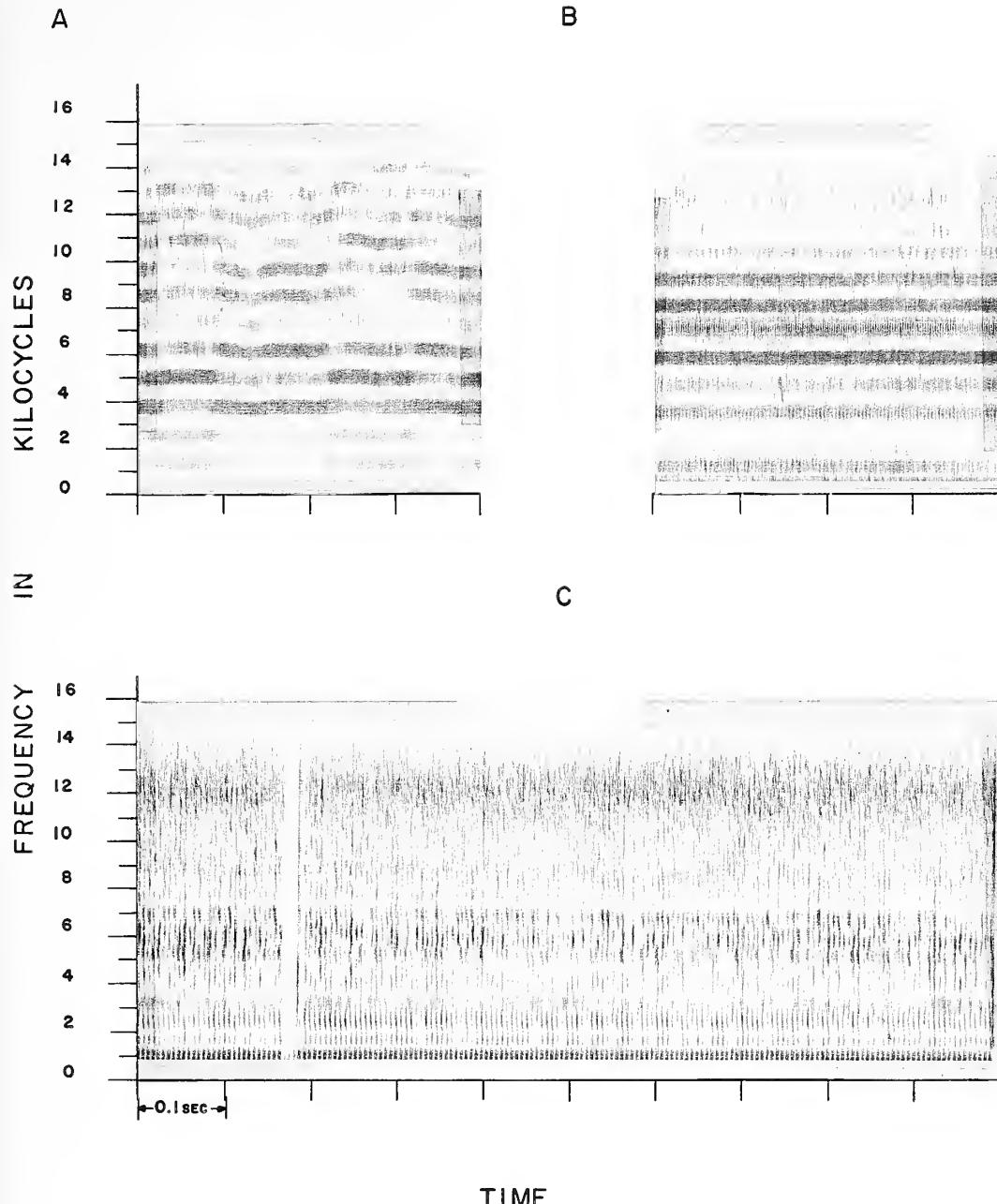
OBSERVATIONS OF THE SOUND PRODUCTION CAPABILITIES OF THE
BOTTLENOSE PORPOISE: A STUDY OF WHISTLES AND CLICKS

OBSERVATIONS OF THE SOUND PRODUCTION CAPABILITIES OF THE
BOTTLENOSE PORPOISE: A STUDY OF WHISTLES AND CLICKS

PLATE IV

OBSERVATIONS OF THE SOUND PRODUCTION CAPABILITIES OF THE
BOTTLENOSE PORPOISE: A STUDY OF WHISTLES AND CLICKS

12
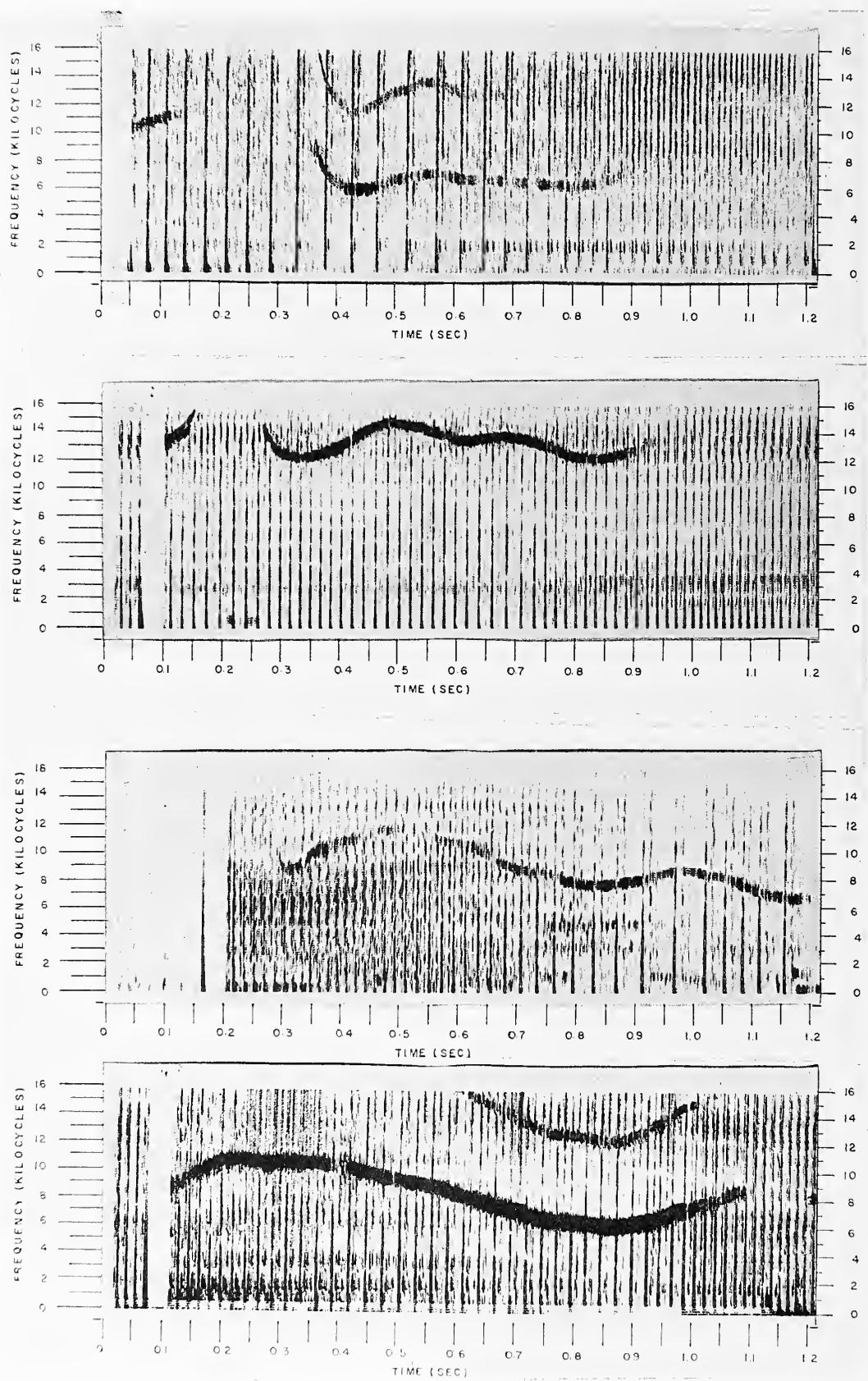
Notes on the Biology of Some Trinidad Swifts[1]

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(Text-figure 1)

THE biology of the neotropical swifts is not well known. For the genera *Chaetura* and *Cypseloides*, with which this paper is concerned, only Beebe (1949), Haverschmidt (1958) and Sick (especially 1948, 1951, 1958, 1959) appear to have made significant recent contributions. They are difficult birds to watch and many are difficult to identify in the field. Several species have never been found nesting.

Compared with the mainland of South America, where, to judge from published data, it is unusual for several species to be common in the same area, Trinidad is especially suitable for field studies of swifts. Here, on an island measuring some 50 by 30 miles, seven species are resident: five of them are known to breed and all seven probably do so. Only one species can be called rare. Probably nowhere else in the neotropical region can so many breeding species of swifts be found in so small an area.

During 4½ years' residence in Trinidad, I made such observations on the swifts as opportunity permitted. They were not a main subject of study, but their abundance brought them constantly to notice. Nests of two species were found in sufficient numbers for a limited analysis of breeding season, number of broods, nesting success and other aspects of breeding biology. In addition, five species were caught in mist-nets, two of them in good numbers, and a sixth was twice caught by hand. This paper presents the information thus collected.

I have followed Lack (1956) in his wide definition of the genus *Cypseloides*. For vernacular names, I have followed Eisenmann (1955) except that I have preferred to use the more evocative name Cloud Swift for *Cypseloides (Streptoprocne) zonaris.*

Distribution, Status and Feeding Habits

The Chaetura Species

The Short-tailed Swift (*C. brachyura*), Band-rumped Swift (*C. spinicauda*) and Gray-rumped Swift (*C. cinereiventris*) are all common species, but they have different local distributions. The Short-tailed Swift is the most widespread, occurring all over the island; it is the only species regularly occurring over open country and towns. It may be seen throughout the Northern Range (the range of forested mountains, up to 3,000 feet high, running along the north side of Trinidad), but is less common there than the other two species. The Band-rumped Swift occurs generally over forested country and wooded savanna, in both lowlands and hills. The Gray-rumped Swift is common in the Northern Range; I did not see it elsewhere.

The fourth species, Chapman's Swift (*C. chapmani*), is very little known. Apart from the original series collected by Chapman in 1894, only a few specimens have been collected, in widely scattered localities from Panama to central Brazil (Wetmore, 1957). I several times thought that I saw Chapman's Swift among mixed parties of swifts in the Northern Range, but the first positive evidence was obtained on November 27, 1960, when one was caught in a mist-net at 1,800 feet at the head of the Arima Valley in the center of the Northern Range. Having had the opportunity to examine a living bird in the hand and to note its field characters as it flew away on release, I later was confident that I saw Chapman's Swift on two occasions, once in the same place and once in the lower part of the Arima Valley. But hundreds of the three other *Chaetura* species were examined before these were seen. From these few records, and from Chapman's specimens collected at Valencia at the foot of the Northern Range about six miles east of the Arima Valley, we may conclude that Chapman's Swift is probably resident in the Northern Range in small numbers.

I obtained no evidence for any differences in feeding habits of the three common *Chaetura* species in places where they occurred together, though quantitative observations might eventually show fine differences. All feed regularly from ground level to several hundred feet up. They commonly skim close to the ground in sheltered clearings in the hills, probably because of the abundance of flying insects in such places, and when termites swarm after wet weather they all come low to feed on them. In wet weather great flocks of them move rapidly up and down the valleys and across the watersheds, avoiding the rain-storms.

The Cypseloides Species

Chestnut-collared Swifts (*C. rutilus*) are common in the Northern Range, but they feed much higher than the *Chaetura* species, and presenting only a black silhouette are often less easy to identify with certainty. Because they fly high, they were the only species resident in the Arima Valley never to be caught in a mist-net. They are usually seen in ones or twos, or small parties. Only once were many seen together; on September 3, 1958, large numbers were seen flying around the summit of El Tucuche (3,068 ft.), the second highest peak in Trinidad, and with them only a very small number of four other species. This was a post-breeding aggregation; many were seen to be moulting their wing-feathers.

The Cloud Swift (*C. zonaris*), the largest and most majestic of the New World swifts, is a migrant to Trinidad. The first birds arrive in July (first dates: 1957, end of July; 1958, July 27; 1959, July 14; 1960, mid-July; 1961, July 8). August and September are the months when the greatest numbers are present. By October their numbers have begun to decline, but a few are seen irregularly until February. This probably represents a post-breeding dispersal from breeding areas in the Andes of Venezuela to the west of Trinidad. A number of specimens collected by Roberts (1934) on August 28 were all completing their moult. I obtained three specimens, in late July and early August; all appeared to be juveniles and were not moulting.

Cloud Swifts are erratic in their appearance, being present in great numbers one day and absent the next. They feed at all heights, and range rapidly and widely over the island. It is likely that at least on occasions they spend the night in the air, as the European swift *Apus apus* has been found to do. On August 11, 1957, I watched a large flock at dusk in the Arima Valley, in the center of the Northern Range. They were spiralling upwards, gradually drifting out of sight behind some hills. Some at least were still circling when poor light prevented further observation. Cloud Swifts roost on cliffs, in clefts and behind waterfalls (Sutton, 1951). There are few suitable cliffs in Trinidad, except the sea cliffs of the north coast, and it seemed unlikely that the large flock I was watching could all have found roosting places for that night.

Belcher & Smooker (1936), on rather unsatisfactory evidence, record another migrant swift for Trinidad, the Black Swift (*C. (Nephoecetes) niger*). This species would be expected to occur occasionally on passage, and further observation may confirm that it does so.

Other Species

Panyptila cayennensis is widespread in small numbers, breeding from near sea level to at least 1,000 feet in the Northern Range. My records of its nests are all in the northern and eastern parts of Trinidad, but the other parts of the island were visited much less often. *Panyptila* feeds high above the ground and is usually only to be identified with binoculars.

Reinarda squamata is confined to savanna and swamp forest in the east of Trinidad, following the distribution of the palm *Mauritia setigera,* on which it nests. It commonly feeds close to the ground.

THE BREEDING OF *Chaetura brachyura*

Nest-site

Belcher & Smooker give the only previous records of the nesting of the Short-tailed Swift in Trinidad. They reported one nest in a chimney, with 3 eggs on June 20, and one nest in a sea cave, with 3 eggs on June 3. There are no breeding records from elsewhere, but observations by Bond (1928, and *in litt.*) suggest that Short-tailed Swifts nest in chimneys in St. Vincent.

I discovered a small breeding colony of Short-tailed Swifts by chance on May 7, 1957, when, watching swifts flying low over bushy savanna near Valencia, I saw a bird suddenly drop out of sight in the grass. I found that it had entered a concrete man-hole, part of an abandoned drainage system constructed during the war when this savanna was the site of a U.S. Air Force camp. A search made in the immediate area revealed eight other man-holes which swifts could enter, and three more were eventually found on other parts of the savanna. These holes were kept under regular observation until September, 1961, giving complete records for five breeding seasons.

Some other breeding sites were found. Short-tailed Swifts were seen during the breeding season entering and leaving sea caves in the rocky north coast of Trinidad, and in Huevos Island off the northwest corner of Trinidad, but no accessible nests were found. One pair was found nesting in a chimney in Arima. Finally, a pair nested for two seasons in a nest-box which I erected 30 feet up against the trunk of a large Chataigne tree (*Pachira insignis*), 500 feet above sea level in the Arima Valley.

The use of this nest-box was unexpected, as all previous records of their nests had been in caves, man-holes or chimneys, and the species is less characteristic of forest than the other *Chaetura* species. The history of its occupation was as follows. On July 9, 1959, a pair of Band-rumped Swifts had been observed entering a natural cavity some 30 feet up in the trunk of this tree, and from observations made on July 11 it was clear that they were feeding young. A ladder was put up to the hole, but the nest could not be seen. The entrance was narrow, and the hole was irregular and descended several feet. Since Band-rumped Swifts had never been found nesting, I subsequently blocked up the natural hole and fixed a nest-box near by, 5 feet long and 1½ feet square in section, with a slit-shaped hole near the top about 5 inches wide (about one inch wider than the tree-hole). Occupation of the box was first noted on June 22, 1960, when a pair of Short-tailed Swifts were found to be feeding five half-grown young. In 1961 a pair of Short-tailed Swifts again nested in the box. In both years a pair of Band-rumped Swifts, presumed to be the former owners of the tree-hole, were several times seen about the tree. It seems that, in making the hole of the box a little wider than the tree-hole, I inadvertently made it big enough for Short-tailed Swifts to enter and they were thus able to dispossess the smaller Band-rumped Swifts (the mean wing-length of the two species differs by about 17 mm.). It is probably because of their larger size that Short-tailed Swifts normally nest in caves and man-made cavities, while the smaller *Chaetura* species, as far as known, nest in tree-holes.

It was of interest that when the Short-tailed Swifts left the box after feeding the young, they used to fly off down the valley in the direction of the savanna three miles away. They would return from the same direction.

Breeding Season

When I first found the nesting colony in the man-holes in early May, 1957, nests were being built and none had eggs until a week later. Table I shows the monthly distribution of the 86 nestings recorded at this colony in the five years. Breeding begins in April or early May and continues until August or early September (the three breeding dates obtained at other sites, and Belcher & Smooker's two records, all fall near the middle of this period). Numbers were too few to reveal slight annual variations, but there were no marked differences in breeding season in the five years.

There was usually a regular succession of nestings in each hole in the course of the breeding season, either in the same nest or, less often, in a succession of nests. No hole ever contained more than one occupied nest at the same time. The intervals between the nestings suggested, as would be expected, that these were normally successive layings by the same female. Combining all the years, two holes were used four

TABLE I. Breeding Season of *Chaetura brachyura*

		Number of nests started in half-monthly periods				
	1957	1958	1959	1960	1961	all years
April 1			1			1
2		1			1	2
May 1	5	4	1	3	1	14
2	4	3	2	3	2	14
June 1	1			4	3	4	12
2	1	1	5	1	2	10
July 1	3	2		1	3	9
2	1	4	2	1	1	9
Aug. 1	3		1	2	3	9
2					3	3
Sept. 1	1	1			1	3
Totals	19	16	16	14	21	86

times in a season, six holes three times, 22 holes twice, and 13 holes only once. These nests suffered a very high rate of predation, which undoubtedly raised the number of nesting attempts above what would be usual in a more successfully breeding population. If we consider only the nine cases where the first nesting attempt was successful, five were followed by a second laying and four were not. The breeding season is hardly long enough for three broods to be reared successfully.

Clutch-size

Chaetura species are known to have, for swifts, very large clutches, and the Short-tailed Swift is no exception. The mean number of eggs in 41 clutches was 3.6 (Table II). Mean clutch-size probably decreases in the course of the breeding season, since the only clutch of six eggs and all the clutches of five were laid in May.

TABLE II. Clutch-size of *Chaetura brachyura*

	Number of nests with clutch-size of					
	1	2	3	4	5	6
April 2				1		
May 1			2	2	2	1
2			3	3	2	
June 1		2	2	1		
2	1		2	1		
July 1			2	3		
2			2	2		
Aug. 1			3	2		
2						
Sept. 1			1	1		
All months	1	2	17	16	4	1

It was not possible to obtain exact data on the intervals between the laying of successive eggs, as my visits were not frequent enough, but incomplete data for ten nests showed that the normal interval is probably two or three days and longer intervals are not uncommon.

A clutch of nine eggs has been omitted from Table II, as it was certainly laid by more than one female. Apart from the abnormal size of the clutch, it could hardly have been laid by one bird as all nine eggs were laid within 14 days. It was of interest that the eggs were incubated successfully, though they were two or three deep in the nest; all nine hatched at about the same time. There was another instance in which the circumstantial evidence was strong that two females were laying in the same nest. Three eggs were laid between 0830 hours on June 1 and the afternoon of June 3, an abnormally quick rate of laying for a single bird. All three eggs were found broken below the nest on June 3, suggesting that the two birds were in conflict. For *Chaetura andrei*, Sick (1959) has reported a similar case of more than one female laying in the same nest. Such cases are presumably attributable to shortage of nest-holes.

Incubation and Fledging Periods

Because the colony was as a rule visited weekly, it was not possible to obtain incubation periods for most of the nests. But more frequent visits were made over limited periods, with the result that for three nests the incubation periods (from the laying of the last egg to the hatching of the last young) were found to be 17 ±1, 17-18 and 18 ±1 days. None of the less exact records was inconsistent with a 17-18 day incubation period.

Fledging periods were difficult to ascertain for the additional reason that the inspection of nest-holes near the fledging time was liable to cause the young to leave prematurely. Also it was found that the young birds return to their nest-hole by day after their first flight. Thus only very careful, repeated observations would show with certainty when undisturbed young first fly.

With these reservations, partial information was obtained on the fledging periods at eleven nests. At five of them, the young flew out on inspection at the ages of approximately 28, 29, 29, 32 and 34 days. One of those that flew when 29 days old was caught as it struggled to rise clear of the long savanna grass and was found to have a wing-length of 112 mm., 8 mm. shorter than the mean adult wing-length. At the six nests where there was no evidence of disturbance, the young left as follows:

(1) one of the two at 29-32 days, the other at 32-36 days.

(2) the first young at 32-36 days, the other two at 36-40 days.

(3) one of the two at 34-38 days, the other after 38 days.

(4) all four young before 35 days.

(5) both young at 35-42 days.

(6) the first two young before 36 days, the third after 36 days.

To sum up these observations, the young can fly if disturbed as early as 28 days after hatching; if undisturbed, they do not usually leave until they are 30-40 days old.

Like Chimney Swifts (*Chaetura pelagica*), young Short-tailed Swifts climb out of the nest while they are still unfeathered and cling to the wall near the nest. At one nest, one of the four nestlings was found clinging to the outside of the nest when 15 days old, the other three still being in the nest-cup. Two days later, at the age of 16-17 days, all four were clinging to the wall a few inches below the nest. At other nests the young were not recorded leaving the nest until three or four days later than this.

Intervals between Broods

The intervals between the ending of one nesting attempt and the laying of the first egg of the next clutch could not usually be ascertained exactly, but 27 intervals were known to within 4 days. These were as follows:

after successful fledging of previous brood: 4, 12, 13, 18, 24.

after loss of eggs: 9, 10, 10, 15, 17, 19, 24, 24, 27, 27, 31, 32, 32, 32, 35, 51, 74.

after loss of young: 17, 19, 29, 51.

Over half of the intervals are between 10 and 30 days. Some of the very long intervals may be false, due to the fact that an intervening clutch had been started and lost between my visits. Because of the variability of the intervals, the number of records is rather small for any certain conclusions, but there is a suggestion that relaying usually follows more quickly after the successful fledging of a brood than after a failure.

Nesting Success

This population of Short-tailed Swifts nesting in underground man-holes was singularly unsuccessful in its breeding; only 15 (17%) of the 86 recorded nestings resulted in fledged young. Usually eggs vanished soon after they were laid, but some losses occurred at all stages. However, hardly any information was obtained on the causes of failure. The possibility was not excluded that snakes and lizards could get into the holes and attack the nests, but there was no evidence that they did so. The only certain predator was a large spider (*Mygale* sp.). When I accidentally dropped two newly hatched nestlings on the floor of the hole, one of these spiders rushed out of a crevice, seized one of the nestlings before I could pick it up, and retreated back to its lair. The squeaks of the nestling ceased the moment it was seized and it appeared to be dead within a second. As this large spider can climb vertical walls it could be a regular predator of small nestlings.

Three nest-holes regularly filled with water after heavy rain, and several nests, as well as at least three adults, were lost in this way.

These observations can, however, have little significance in the ecology of the species as a whole. Underground man-holes must be such an unusual nest-site for the Short-tailed Swift that neither the high rate of nest failure nor the causes of failure are likely to be typical.

The Moult, and Roosting Habits

Two birds trapped on August 14, one caught on September 16, eight on September 18, and one on September 25 were all in various stages of moult. Only three other adults were caught, one in March and two in July, and none of these was moulting. Details of the sequence of moult are given in a later section.

At 1000 hours on September 16, 1957, a fine sunny day, one of the nest-holes which had not been in use for some weeks was found to contain about 50 adult swifts. On September 25, 50 birds were again found in this hole at 1020, and ten were found in another hole containing a nest with eggs, apparently deserted. The birds caught on these two days were in moult, as has been mentioned above. Subsequently it was found that during the moult the adults regularly spent part of the day in two or three of the holes, either clumped, as at night, or clinging scattered on the wall.

I visited the colony at night several times and found the swifts roosting in the holes all the year round, but in the months November-March their presence was irregular. Outside the breeding season, they tended to congregate in two or three holes, the same ones that they were found in by day during the moult, roosting in clumps of 30 or more birds together. As the breeding season approached their numbers declined, the roosting aggregations broke up, and each hole was finally occupied at night by a pair or three birds. As late as February, up to 50 birds were found roosting in the nine holes inspected; by early May the numbers had fallen to 21.

When disturbed at night, Short-tailed Swifts give the same wing-clattering display as has been described for the Chimney Swift (Fisher, 1958). The birds slowly raise their wings above the back, then spring away from the wall with a clattering sound, to land back in the same spot or a few inches away. The clattering appears to be made by the rapid clapping together of the wing-tips. Several birds in a clump will raise their wings together and clatter at the same time, so that the noise is quite startling to the intruder. There seems no doubt that it is an anti-predator display analogous to the hissing of tits and some other hole-nesting birds. After a few bursts of clattering a roosting clump becomes broken up, with the birds more evenly scattered over the sides of the hole.

Breeding, Moulting and Roosting of Other *Chaetura* Species

Extremely scanty information was obtained on the other *Chaetura* species. For Chapman's Swift nothing was found out except that the individual caught on November 27, 1960, was undergoing slight body moult.

For the Band-rumped Swift there were only two observations of note. On July 9 and 11, 1959, as already mentioned, a pair was found to be feeding young in a hole about 30 feet up in the trunk of a Chataigne tree (*Pachira insignis*). This is the first indication of the breeding site of the species. A flash photograph of Short-tailed Swifts roosting in one of the manholes on February 27, 1958, showed the presence among them of a single Band-rumped Swift. This appears to be the first record of roosting for the species.

More information came from the trapping program. Twenty-one Band-rumped Swifts were caught in mist-nets in the Arima Valley, 6 in January, 1 in February, 1 in April, 2 in August, 8 in October and 3 in November. One caught on August 3 was finishing its wing-moult, the two outer primaries not being full-grown. Another, caught on October 23, was probably just finishing its wing-moult as some of the primary coverts were growing but not the primaries themselves, which were fresh. These were the only examples of wing-moult. Eleven of the 17 birds trapped in the months October-January were undergoing body-moult. The weights of these trapped birds are given in the Appendix.

For the Gray-rumped Swift even less information was obtained from field observation. I once almost certainly saw a pair enter a cleft in an Immortelle tree (*Erythrina micropteryx*) about 1,000 feet above sea level in the Arima

Valley at dusk, but the light was so bad that when the birds, which I had under observation for half an hour as they circled the tree, finally entered, or appeared to enter, the hole, I could not be certain of what I had seen.

Forty-three Gray-rumped Swifts were caught in mist-nets, in several months of the year. An analysis of the moults of these birds is given in Table III. It will be seen that 9 of the 13 birds trapped between June 14 and November 6 were undergoing wing-moult, but none of the 29 birds trapped from January 5 to May 26. The bird trapped on May 26 had an incubation patch and weighed 16 gm., the highest weight recorded (see Appendix), and so was clearly laying eggs. This evidence suggests that the Gray-rumped Swift has much the same breeding season as the Short-tailed Swift.

Table III. Moult Data for Trapped
Chaetura cinereiventris

	Number of individuals showing		
		Body-moult	
	Wing-moult	only	No moult
Jan.		14	2
Feb.		2	
April		4	6
May			1
June	1		1
July			1
Aug.	1		
Oct.	3		
Nov.	4		2

The Moulting Sequence in *Chaetura*

Nine moulting Short-tailed Swifts were examined, nine moulting Gray-rumped Swifts, and one moulting Band-rumped Swift. The wing-moult follows the pattern that is general in many birds; the primaries moult in sequence from inside outwards and the secondaries centripetally from the two ends. For the primary moult, which spans practically the entire period of the moult, the following stages are recognized, using a method of notation adapted from Miller (1961): Stage 1, 1st (innermost) primary growing, 2-10 old; Stage 2, 2nd primary growing, 3-10 old; and so on to Stage 9, 9th primary growing, 10th old; Stage 10, 10th primary growing.

The secondaries are much shorter than the primaries and their replacement is much more rapid. They do not begin to be moulted until the primary moult is well advanced, and they finish before the primaries finish. No difference was noted between the Short-tailed and Gray-rumped Swifts in this respect. Three birds were examined whose primary moult was at Stage 6;

all had old secondaries. Two were examined at Stage 7; in one the secondaries had begun to moult, but not in the other. Three at Stage 8 were all replacing their secondaries. Two at Stage 9 and two at Stage 10 had all finished replacing them.

The tail moults centripetally. It begins after the primary moult has begun and ends at about the time that the primary moult ends. In the Short-tailed Swift it seems, by extrapolation from the specimens examined, that the tail begins to moult at Stage 4 or 5 in the primary moult, but no birds were examined at these stages. In the Gray-rumped Swift the tail moult begins later, at Stage 7 or 8. This difference between the two species is apparent from the following comparison of birds at the same stages of primary moult:

	Short-tailed Swift	Gray-rumped Swift
Stage 6.	Two birds, both half way through tail-moult	One bird, tail not moulting
Stage 7.	Two birds, about three-quarters through tail-moult	—
Stage 8.	One bird; tail-moult nearly complete	Two birds; one just starting tail-moult, the other half way through
Stage 9.	One bird; tail-moult complete	One bird; tail-moult nearly complete
Stage 10.	—	Two birds; tail-moult nearly complete

Besides being less regular in its sequence than the wing-moult, the tail-moult is also sometimes not complete. Two birds that were not moulting showed incomplete replacement of the tail-feathers: in one the outermost pair of feathers, and in the other the central pair, were old and worn, the rest of the tail-feathers being new.

THE BREEDING OF *Cypseloides rutilus*

Belcher & Smooker give records of three clutches, from two nests, and Orton (1871) mentions the nest-site. These appear to be the only breeding records published for the Chestnut-collared Swift. During the present study ten occupied nests were found, and two other unoccupied nests. Nests are usually repaired and used year after year, and the ten occupied nests gave records of 33 nestings.

Nest and Nest-site

The nest is a substantial bracket, semicircular in horizontal section, with a shallow depression for the eggs. It is made of various plant fibres, usually including some moss, and is fixed, presumably with saliva, onto a smooth rock-face or wall, a few feet above water. The natural nest-sites in the Northern Range of Trinidad are vertical or overhanging rock-faces at the sides of mountain streams or gorges; eight nests were found in such sites. In addition, one nest was found under a bridge, about 16 feet above the water, and two were found in culverts, through which small streams flow under the main road that runs up the Arima Valley.

The remaining nest was in a small sea cave on the north coast. Owing to the collapse of its roof, this cave had become a hole with a low tunnel leading through to the sea. The nest was situated 7 feet up, under an overhang above the landward end of the tunnel. Chestnut-collared Swifts were also seen during the breeding season entering and leaving La Vache cave on the north coast, a large sea cave occupied by Oilbirds (*Steatornis caripensis*), and flying out of a sea cave on the north side of Huevos Island, off the northwest corner of Trinidad. There are many caves along the north coast of Trinidad and the off-lying islands, and doubtless Chestnut-collared Swifts breed in them in considerable numbers.

Breeding Season and Breeding Statistics

The breeding season is much the same as that of the Short-tailed Swift; the first eggs were laid in April or May in each year, and the last in August. The date of laying of 32 clutches is shown in Table IV (one nest could not be dated accurately enough for inclusion). Is is curious that two of Belcher & Smooker's three clutches fall outside these limits. One of them was accurately dated August 31-September 2, only a little later than the latest of my nests; the other was found on November 10. The possibility that the

TABLE IV. Breeding Season of *Cypseloides rutilus*

	Number of nests started in half monthly periods
April 2	1
May 1	3
May 2	3
June 1	4
June 2	4
July 1	2
July 2	6
Aug. 1	5
Aug. 2	4

latter was an old deserted clutch is not mentioned.

In all cases except one, the clutch was two eggs. The interval between the laying of the two eggs was not accurately determined, but at one nest it was at least two days and the other records are all consistent with a two-day interval between eggs.

The single clutch of one egg was laid in circumstances that suggested a bird breeding for the first time. The nest was begun in June, 1961, in a site that was known not to have been used for at least four years, as the place had been under fairly frequent observation. Building was slow and was hindered by heavy rain which caused part of the nest to fall away. The nest was finally completed by the third week of August and the single egg was laid a few days later.

The incubation period (from the laying of the second egg to the hatching of the second young) was ascertained at three nests to be 22, 22-23 and 24 days. Fledging periods were ascertained to within a few days at four nests, and were found to be 37-44, 38-40, 39-40 and 39-41 days. At another nest the date of hatching was not known, but the period from the laying of the second egg to the flying of the two young was found to be 60-63 days.

Two of the nests that were followed through a complete breeding season were used only once, ten were used twice and one was used three times, the first two attempts being unsuccessful and the third successful. The season would not be long enough for three broods to be reared.

The most complete record was obtained for one nest-site that was occupied for five successive years, though eggs were not laid in it in the fifth year. Two broods were reared in 1957, two in 1958 and one in 1959. In 1960 the first brood was reared and a second clutch was laid but was lost soon afterwards. In the off-season 1960/61 the nest, which was only about four feet above the water of a rock-bound pool in a mountain stream, was washed away. Another nest was built in April, 1961, a few feet away, but even nearer the water; it remained empty for several weeks, then it too was washed away in July. The bird returned to the old site and built a new nest in late July and August; but probably by then the season was too far advanced and no eggs were laid in it. The history of this nest-site in shown graphically in Text-fig 1.

Intervals between broods (from the flying of the young to the laying of the first egg of the next clutch) were rather short. Those that were known to within a range of six days were as follows: 4-8, 5-11, 6-11, 9-11, 10-13 days. In
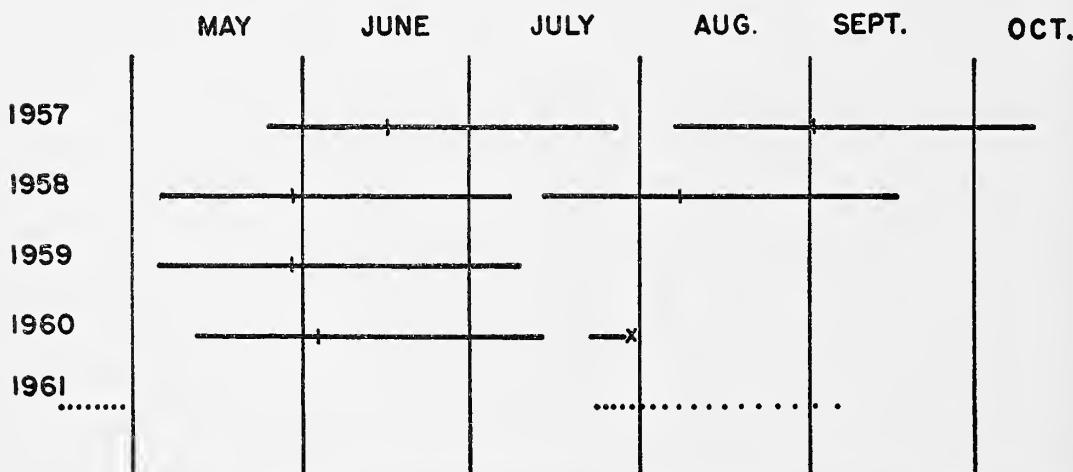
TEXT-FIG. 1. Occupation of a Chestnut-collared Swift nest-site over five breeding seasons. Each nesting is indicated by a heavy line, and the hatching date by a short bar. Dots: nest-building. For further details see text.

addition there was one instance of the first egg of the second clutch being laid 3-5 days before the single nestling of the previous brood left the nest. The two intervals following loss of eggs were longer than those following successful fledging: 13-17 and 21-23 days.

Chestnut-collared Swifts' nests seem to be safe from predators, and breeding success was fairly high: 15 (63%) of the 24 nestings which could be used for analysis resulted in fledged young. Two clutches were soaked by water running down the rock-face after heavy rain and were abandoned. The eggs or young disappeared from six nests, and one was deserted for no known reason. Although the hatching rate was high in the successful nests (27 out of the 29 eggs that survived to the expected date of hatching), there were a few losses of eggs during incubation, and some losses of young at all stages, and the mean number of young leaving 18 successful nests (all of which had clutches of 2 eggs) was 1.3.

An estimation of the reproductive rate can be made from these figures, which there is no reason to think are untypical. If the mean number of nesting attempts per year is taken to be two, nesting success is 63%, and the number of young fledging from successful nests is on average 1.3, each breeding pair will rear on average 1.6 young per year.

Adaptations to Cliff-nesting

There is suggestive evidence that birds which nest in safe sites tend to have longer incubation and fledging periods than related species nesting in sites more exposed to predation, presumably because the selective pressure for quick development is relaxed (Lack, 1954). This may be part of the reason for the long incubation and fledging periods of the Chestnut-collared Swift compared with *Chaetura* species, which are almost certainly tree-hole nesters by origin.

If clutch-size is limited by the number of young that can be fed, a reduction in the rate of development of the young will enable clutch-size to be increased. As Lack points out, there is good evidence that this has happened: passerines with safe nest-sites tend to have not only slower rates of development but also larger clutches than passerines with exposed nest-sites. The small clutch of the Chestnut-collared Swift and of other *Cypseloides* species (Lack, 1956), compared with *Chaetura* species, is contrary to this rule. Probably it is due to the nature of the nest-site. *Chaetura* nestlings climb out of the nest when half-grown, so that large families can be reared from their small nests, but it would be impossible for half-grown Chestnut-collared Swifts to cling safely to the smooth, often overhanging rock-faces to which the nest is fixed,

and two full-grown young are as many as can be accommodated on the flattish top of the nest. Towards the end of their nestling period they exercise their wings while hanging to the outer rim of the nest, a method also recorded for the Black Swift (Bent, 1940).

An alternative explanation for the small clutch-size in *Cypseloides* is that their method of feeding is such that they are unable to find food for more than one or two nestlings. As mentioned above, Chestnut-collared Swifts feed higher than the *Chaetura* species, and the density of flying insects must in general decrease with altitude. The point cannot be ruled out, yet it seems unlikely that in many different habitats, and over a wide range of latitude, *Chaetura* species are always about three times as efficient at collecting food as *Cypseloides* species.

Lack (1956) has stated that among swifts only the Hemiprocninae and *Cypsiurus* develop nestling down, presumably for warmth and camouflage, as they nest in exposed sites. But downy young have been recorded for the Black Swift (Bent, 1940), and in the Chestnut-collared Swift, too, the nestling develops thick down. Like the Black Swift, the Chestnut-collared Swift is hatched naked and grows its down after a few days; Table V gives details of the development of a nestling whose exact age was known. Presumably in *Cypseloides* the nestling down is primarily an adaptation for heat conservation. The shady and damp places where they nest are several degrees colder than the surroundings.

HOVERING FLIGHT IN *Cypseloides* AND *Chaetura*

It does not seem to have been recorded that some swifts on occasion adopt a hovering method of flight in which the wing action must be more like that of a hummingbird than of a swift in normal flight. During night visits to the Oilbird colony in the Arima gorge, roosting Chestnut-collared Swifts were sometimes disturbed by my torchlight and would fly slowly about the cave with a hovering flight, the body being rather upright, until they came in contact with a rock-face to which they could cling. Twice I easily caught a bird as it hovered slowly towards me and clung to my clothing. In the same gorge in the day-time Chestnut-collared Swifts, when disturbed from their nests, would fly off with the usual rapid flight, as do those disturbed from nests in more open places along streams. Limited observations suggested that they normally also fly to their nests with rapid flight. Under undisturbed conditions, the hovering flight is probably used by the swifts when going to roost in caves and dark gullies at dusk.

TABLE V. Development of Nestling Chestnut-collared Swift

Date	Age	Description
3 June	Just hatched	Naked; skin pink; down rudiments visible as dark spots on upper surface.
6 June	3 days	Down visible as blackish streaks, not yet through skin.
9 June	6 days	Down beginning to sprout on upper surface. Rhythmic clutching movements with feet when removed from nest.
13 June	10 days	Eyes just open; gray woolly down all over upper surface, much sparser on underside.
17 June	14 days	Thick down above and below. Primary and secondary coverts up to 1 mm. out of sheath; primaries and secondaries as long pin-feathers.
22 June	19 days	Thick down all over body; feathers in sheath beneath down; front half of head feathered, feathers of fore-crown sooty with rusty fringes; wing-feathers 10-15 mm., tail-feathers c. 5 mm. beyond sheaths.
27 June	24 days	Head well feathered; wing- and tail-feathers well grown.
8 July	35 days	Nearly ready to fly; collar dull rufous.
11 July	38 days	Still in nest in late afternoon.
14 July	41 days	Nest empty.

and perhaps going to nests in clefts where a straight run-in is not possible. Its value in allowing safe flight in dark and confined places is obvious.

Short-tailed Swifts were seen to use the same hovering flight when rising vertically out of the man-holes where they nested. As they rose clear of the hole they at once changed to the usual rapid flight and flew off low, skimming the grass. *Chaetura* species must always fly thus when they leave narrow chimneys or other cavities with a top hole.

SUMMARY

The breeding and other aspects of the biology of swifts of the genera *Chaetura* and *Cypseloides* were studied in Trinidad, West Indies. The status of the five resident and one migrant species is summarized.

A small breeding colony of *Chaetura brachyura* was kept under observation for five breeding seasons. The breeding season extended from April to early September. Most birds made from one to three nesting attempts in each season. Mean clutch-size was 3.6 eggs, the incubation period was 17-18 days, the fledging period 30-40 days. Breeding success was low, but was considered not to be typical, owing to the unusual nest-sites (underground sewer manholes). After the breeding season, moulting birds often spend part of the day clumped together in the nest-holes.

Data are presented on weights and measurements of *Chaetura brachyura, C. cinereiventris* and *C. spinicauda,* and on the sequence of moult in *C. brachyura* and *C. cinereiventris.*

Data are given on 33 nestings of *Cypseloides rutilus,* nesting on overhanging cliffs above streams, under bridges and culverts, and in sea caves. The species is single or double brooded, and repairs and re-uses its old nests year after year. The clutch normally consists of 2 eggs. Incubation lasts 22-24 days, and the fledging period is about 40 days. The young is hatched naked, but develops a thick covering of down. The small clutch, the long development period and the nestling down are all considered to be correlated with the specialized nest-site.

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APPENDIX
WING-LENGTHS AND WEIGHTS

The figures in parentheses give the number measured, and are followed by the range and the mean.

Weights were recorded immediately after capture, except where specified. Wings were measured in the normally closed position, the primaries retaining their natural curvature.

Chaetura brachyura

Wing (10) 116-130, 119.9 mm.
Weight (11) 17-30, 19.8 gm.

The large weight-range is due to a single bird of 30 gm.; all the others were between 17 and 22 gm. This very heavy bird, a female, was caught on March 22, about six weeks before breeding began; it was very fat, the ovary being still quite small. The other birds were all caught in August and September.

Chaetura cinereiventris

Wing (37) 98-105, 101. 5 mm.
Weight (43) 12.5-16. 13.8 gm.

Chaetura spinicauda

Wing (19) 98-107, 102.6 mm.
Weight (21) 13-18, 14.2 gm.

Chaetura chapmani

Wing (1) 120 mm.
Weight (1) 25.5 gm.

Cypseloides rutilus

Weight (2) 20, 22 gm.

The lighter of the two birds was captured in the evening and weighed early next morning.

Cypseloides zonaris

Weight (3) 60, 63.5, 74 gm.

The two lighter birds had been knocked down with sling-shots from a low-flying flock and had been several hours without food when weighed.

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The Genetics of Some Polymorphic Forms of the Butterflies
Heliconius melpomene Linnaeus and *H. erato* Linnaeus. I. Major Genes.[1,2]

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(Plate I; Text-figure 1)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended principally for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I." by William Beebe, Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.]

CONTENTS

I. INTRODUCTION

THE neotropical butterflies *Heliconius melpomene* and *H. erato* (Lepidoptera, Nymphalidae, Heliconiinae) show complex parallel polymorphism in their wing markings (Oberthür, 1902; Eltringham, 1916; Joicey & Kaye, 1916). In connection with research into the biology of the heliconiine butterflies of Trinidad[4], the genetics of several of the polymorphic forms of *H. melpomene* has been investigated. Crosses were made between several forms bred from eggs obtained in the wild in Surinam (Dutch Guiana) and between the Surinam stock and insects from Trinidad, West Indies, where the species is monomorphic. The results show that most of the differences between the major polymorphic forms studied are produced by genes in the same linkage group; analysis of previously described broods of *H. erato* (Beebe, 1955)

shows that the mode of inheritance of analogous patterns in this species is very similar to that in *melpomene*.

This paper deals with differences produced by major genes; a second paper will deal with quantitative variation (Turner, in press).

The preliminary work involved in assembling the material was long and exacting. The difficulties included irregular seasonal scarcities, the intermittent prevalence of disease, the apparent impossibility of hand-pairing the imagos, the usually rapid deterioration of the stock with inbreeding and, finally, the fact that the larvae, being not only non-gregarious but incompatible, had to be reared singly. We would like, therefore, to express particular thanks to the people responsible, through parts of two years at the Trinidad Field Station, for the collection of the stock and the rearing of the resultant broods. Included are Mr. Henry Fleming, who collected the breeding stock on field trips to Surinam and who designed the breeding cages, and the following laboratory assistants: Mesdames Susan Allan, Kathleen Campbell, Frances W. Gibson and Jane S. Kinne, and Misses Constance Carter and Diana Jeffrey.

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Finally, we express our indebtedness to the late Dr. William Beebe for his continued and constructive interest in the general study of the biology of the heliconiines and for his helpful suggestions in the course of the present section of the work.

II. THE GENETICS OF *H. melpomene*

A. MATERIALS AND METHODS

1. *Methods of Collection.* Most of the material for the present contribution was collected in Surinam in December, 1958, and during the same month in 1959. Rearing and breeding were carried out at the Trinidad Field Station. Crosses between Surinam material and *melpomene* from Trinidad were produced by mating stock living near the field station with broods resulting from the eggs and larvae collected in Surinam.

In both years the Surinam collections were made during pronounced dry seasons in the vicinity of Moengo, a bauxite mining community in the northeastern part of the country. Some were taken near the wharf and others close to the Moengo end of a 30-mile road joining Moengo and Albina. The latter town borders the Maroyne (=Maroni) River which separates Surinam from the region of French Guiana from which came the collection described by Joicey & Kaye (1916). The Moengo area has become so well known to us over a period of years that individual food plants, located in previous seasons in an area of some 20 square miles, could be revisited daily.

Eggs and larvae of *H. melpomene* were exceedingly scarce during the two collecting periods under consideration, each of which lasted one week. The total catch numbered 13 in 1958 and 17 in 1959; each year the specimens were found in only two small areas; 12 of those taken in 1958 came in fact from a single vine. During each year only two or three imagos were seen flying in the entire area of search. It therefore seems likely that the resultant broods came from not more than several females each season.

2. *Methods of Breeding.* A summary of the material is given in Table I. As indicated, the broods resulting from the eggs collected in December, 1958, were exceedingly subject to disease and/or genetic weakness. In the following year therefore it was thought wise to breed pairs in which the males and females in the generation came from localities separated by approximately 10 miles. Abnormalities, particularly crumpled wings and the inability to emerge fully from the pupal case, as well as a number of forms of disease and/or abnormalities in the larvae, frequently appear in the second inbred generation.

Even when inbreeding is avoided, however, as in our nongenetical studies, it is not possible ever to plan definitely to rear particular species of heliconiines, including *H. melpomene,* in any given season, because of the frequent occurrence

TABLE I.

Year	Eggs Laid	Eggs Hatched	% Hatched	Larvae Successfully Reared	% Larvae Successfully Reared of Eggs Laid	% Larvae Successfully Reared of Eggs Hatched
1959	248	227	91.6%	25	10.1%	11%
1960	2,605	1,832	70.4%	777	29.8%	44.7%

of disease. Sometimes a year of abundance is followed by two poor seasons as in the material under consideration; sometimes good and poor years alternate; rarely do two good years follow each other. Evidence is accumulating that poor seasons occur simultaneously in Surinam and Trinidad, and that both the annual amount of rain and the condition of the food plants are involved.

The eggs and larvae collected in Surinam were brought to Trinidad by air and reared in the laboratory by the same general method previously described (Crane, 1955, pp. 168-170; Beebe, Crane & Fleming, 1960, pp. 113-115). Briefly, this consists of rearing each caterpillar in an individual dish, because of the cannibalistic habits of the early instars and the frequent aggressive behavior of larger larvae. Low stender dishes, 60 × 28 mm. in size and with ground glass lids, are ideal containers during the first three to four instars. When adequate space and glassware become a problem the early instars are also reared in 3 × 1-inch vials, with the uncorked mouths pushed into a tray of damp sand. Humidity, a most important factor in the rearing of heliconiines, is difficult to control when the vials are used. In the stender dishes and in the 4 × 4 × 2.5-inch glass refrigerator dishes used for the last one or two instars, humidity is furnished by small sections of cotton dental wads, which are saturated and squeezed partly dry. Larvae also drink from drops of water left on the sprinkled leaves.

The normal foodplant of the species both in Surinam and in Trinidad is *Passiflora laurifolia* L. Eggs have been collected also in the field and reared in the laboratory on three other species of the same genus, *P. auriculata* HBK, *tuberosa* Jacquin and *lonchophora* L.

Before the prepupal wandering phase, larvae for genetical study are furnished with a piece of firm wire netting laid beneath the glass cover of the dish. Healthy larvae climb on the netting and usually spin the pad toward the middle of the screen, pupation normally taking place the following morning. Pupae are kept undisturbed for 24 hours, after which each screen with its label is transferred to the top of a jar or tumbler above a well-soaked cotton wad.

The approximate usual durations of the developmental stages are as follows: Egg, 4 days; larval instars, 15; pupal, 9 to 10. Further details are given in Beebe, Crane & Fleming, *loc. cit.*

The night before emergence, if the imago is certainly not to be bred, the screen with the pupa is transferred to the top of a cylinder made of soft wire netting and set in a dish of damp sand. After emergence the butterfly is allowed to dry

the newly expanded wings for several hours before being placed, wings folded, in a transparent plastic envelope, and chloroformed. About 24 hours later, when *rigor mortis* has passed, the butterfly is removed, the wings opened out flat with forceps, and the insect returned to the envelope. In the absence of a drying cabinet the envelopes may be stored in a cardboard carton and, without uncovering, exposed daily to hot sun or the top of a warm oven. Abundant and constant paradichlorobenzine is a tropical necessity, not only to ward off pests but to prevent mold. The prompt spreading of the wings and storage of the insect in fully transparent envelopes eliminates both pinning and traditional spreading techniques; considerable time is thus saved, while shipping, sorting and study are all facilitated.

Butterflies intended for breeding are treated as follows. Males are released, as soon as the wings dry, into isolation cages of wire mesh measuring at least six feet on a side. When more than one male is kept temporarily in the same cage, the specimens are marked with waterproof, quick-drying lacquer. The males are allowed to mature to the requisite age for mating before being placed in a cage with a female, since courtship is then more likely to take place, particularly between individuals of low vitality. No male mates before the second morning after emergence, at the imaginal age of about 48 hours; 72 hours is the normal age in *melpomene* while 96 hours is occasional. Males are placed singly in breeding cages that measure at least 9 × 9 × 8 feet, preferably on the night before breeding is expected to take place, so that any shock of handling is minimized and time allowed for recovery. The insect should never be picked up between bare fingers or chased with a net; a strip of wax paper will insulate wings from the fingers or a small net may be used after the insect has come to rest.

Females to be bred are placed either in small isolation cages or directly in the breeding cage. Mating can occur in this species at any imaginal age from about 1½ hours to about 12 days. Females are most attractive on the first and second days. Males may be bred at least four times with healthy offspring resulting. They are not known to mate on successive days, although mating is often repeated when one day has elapsed between the pairings. Successful breeding has resulted in males more than two months old.

It has not been found possible to pair any heliconiine by hand[5], and they have not been

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[5]*Dione juno*, which rarely mates or oviposits in captivity, can be hand mated and will readily lay when

mated successfully in cages much smaller than the size specified above. Females will however lay eggs in normal numbers in cages measuring about six feet in each dimension. Single individuals of either sex may be kept when necessary for two or, rarely, three days in cages about three feet on a side; however, they must be fed, beginning on the second morning, with flowers placed on a shelf near the cage top in the brightest corner. If the butterflies are kept longer in such cramped quarters, their vitality proves to be impaired when eventually they are moved to the breeding cages.

Details of the maintenance of butterfly insectaries will be found in Crane & Fleming, 1953, and Crane, 1955, 1957. The principal factors ensuring success, regardless of cage size, are: abundant natural flower food; abundant humidity, maintained through sprinkling when necessary; foliage, or at least growing grass, inside the cage; and ample sun and shade.

No female has ever been found to lay eggs on any plant not belonging to the genus *Passiflora*. The maximum number of eggs laid by a single *H. melpomene* was 196 over a period of fifty-five days. One to four eggs are usually laid per day, rarely more, beginning on the eighth to fifteenth day after emergence. The major egg-laying period is finished after about two weeks; later in the female's life eggless days may become frequent. Eggs are collected every afternoon to avoid predation by ants.

It is doubtless unnecessary to emphasize the importance for care and detail in labelling at every step of the study, from the gathering of eggs, whether wild or cage-laid, to the final labels on the envelopes holding the imagos. Self-adhesive labels are used on the rearing dishes while metal garden markers work well on breeding and egg-laying cages out-of-doors.

3. *Methods of Study*. The wing pattern of *melpomene* is made up of a number of elements which vary independently and which occur in most if not all possible combinations, each one of which has a separate taxonomic name (Seitz, 1913; Joicey & Kaye, 1916). Rather than become involved in nomenclatural difficulties, we have adopted the procedure recommended by Camp and Gilmour (Gilmour, 1958) in another context, of keeping the genetic and taxonomic

names completely separate; this system also has the advantage that the same notation may be used for *H. erato*. The various pattern elements we studied are therefore designated by English names, with appropriate symbolic letters, as follows:—

> Ray (R): the presence of four to six red radiate marks on the discal part of the upperside of the hindwing (Pl. I, Fig. 1);
>
> nonray (r): the absence of such red rays (Pl. I, Figs. 2-5);
>
> Dennis (D): the presence of extensive red areas at the base of the forewings on the upper and under sides, and on the base of the hindwings on the upperside (Pl. I, Figs. 1-3);
>
> nondennis (d): the absence of such red areas (Pl. I, Figs. 4-5);
>
> Wide-band (B): the presence of a broad red band extending from the costal edge of the forewing towards the inner angle (Pl. I, Figs. 1, 2 & 4);
>
> narrow-band (b): the presence of a narrow red band extending from the costal edge of the forewing toward the inner angle (Pl. I, Figs. 3 & 5).

In addition there was much quantitative variation in the width and shape of the forewing bands and in the amount of yellow pigment in the discal area of the forewing, which will be discussed in the second paper (Turner, 1962).

In the course of the present study, Crane has been responsible for the Trinidad aspects, including methodology, pair selection and supervision of rearing and recording. The work of analysis, on the other hand, has been accomplished altogether by Turner at the University of Liverpool.

B. Results

Data for all the broods reared will be found in Tables II and III. In the light of our findings we have deduced the genotypes of most of the parent butterflies, although in some instances, marked with an asterisk, it has been possible only to indicate the most likely genotype, assuming that crossing-over has not occurred. Note that as the Trinidad population is monomorphic all Trinidad butterflies must be homozygous at the major loci.

1. *Inheritance of the Ray Pattern*. The only brood in which this pattern occurred (Table II, 1) shows that it is probably inherited as a single factor, one of the parents of the brood being a recessive homozygote, the other a heterozygote, but it is not possible to tell from the data

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confined in a black silk-organza sleeve. *Heliconius numata* and *H. erato* have been hand mated and the latter has laid in a sleeve. However, both species are refractory in these respects and the techniques are not recommended unless the normal methods have failed.

Table II. Breeding Data for *H. melpomene* (First Series). (1959)

Brood No.	♂ Parent		♀ Parent		Brood			
	Brood or Origin	Phenotype	Origin	Phenotype	BDR	Bdr	bdr	Total
1	Surinam	Bdr	Surinam	BDR	♂ 0	1	0	1
					♀ 3	4	0	7
					3	5	0	8
2	Surinam	Bdr	Surinam	bdr	♂ 0	2	6	8
					♀ 0	3	2	5
					0	5	8	13
3	Surinam	Bdr	Surinam	Bdr	♂ 0	2	0	2
4	3	Bdr	Trinidad	Bdr	♂ 0	1	0	1
5	Surinam	Bdr	Trinidad	Bdr	♂ 0	1	0	1

whether the gene is dominant or recessive; the use of the capital R for the Ray pattern is therefore provisional. For reasons explained under Section 4 below, it is apparent that the locus is not sex-linked.

2. *Inheritance of the Dennis Pattern.* A large number of broods show that this pattern is produced by a single dominant gene which is not sex-linked. For example, in Table III, broods 3, 6 and 27, all of which are D × D, give a satisfactory approximation to the ratio 3 D:1 d. The dominance of the *D* gene is confirmed by brood 23, and broods 14, 22, 24, 26 and 32 among others conform to the 1:1 backcross ratio, so confirming that a single gene is involved. Broods 22, 24 and 26 also show that the gene is autosomal, for if it were sex-linked all males would be nondennis and all females Dennis. The anomalous individuals in brood 7 are assumed to be the result of an error.

3. *Inheritance of the Width of the Bands.* Similarly the difference between a Wide-band and a narrow-band is produced by a single autosomal locus, the factor for Wide-band being dominant. In Table III, among others, broods 4, 9, 10 and 22 are seen to be F_2 generations, corresponding to the 3:1 ratio, broods 13, 23 and 29 are backcross generations and brood 13 demonstrates the absence of sex-linkage. Again the anomalous individual (brood 28) is assumed to result from an error.

4. *Linkage of Ray, Dennis and Band Factors.* The three loci controlling the patterns Ray and Dennis and the width of the band are all in the same linkage group. Thus in Table II, brood 1 is apparently a backcross for the Ray and Dennis factors and departs significantly from independent assortment ($P < .01$ by Fisher's exact test);

there are no crossovers. The maximum crossover value, estimated on the assumption that if one more butterfly had emerged it would have been a crossover, is 11%, with a standard error of ± 11%. It is therefore highly unlikely that the COV is more than 30% and it may be much lower. We stated earlier that the Ray locus was not sex-linked; the reason for this conclusion is now obvious.

The data themselves do not exclude the possibility that the Ray locus is on a separate chromosome from the Dennis locus, but that the *R* gene can only express itself in the presence of the *D* gene; however we think this unlikely, as there is a variety of *H. melpomene* in which the Ray pattern occurs independently of the Dennis pattern (var. *contiguus*, see Eltringham, 1916, plate XII, 26). As this variety apparently occurs only in Ecuador (Joicey & Kaye, 1916: p. 420), it is possible that the COV between *D* and *R* is very low.

Similarly the *D* and *B* loci are linked, as is shown by broods 22 and 24 (*P* for independent assortment less than .0003). If crossovers had occurred they could have been detected by inspection of the phenotypes in broods 4, 15, 17, 22, 24, 27 and 30 (Table III); in these broods no butterflies have appeared in the crossover class (bd) and as at least one, and in some broods probably both parents in each cross are repulsion heterozygotes, it is not possible to obtain a reliable estimate of the crossover value. A total of 11 butterflies from broods 2, 14, 17 and 32 (Table III) has been crossed in such a way that their genotypes can be determined from their progeny; of these, 3 are carrying crossover chromosomes, two of them *bd* and one *BD* (the original chromosomes in the crosses

TABLE III. BREEDING DATA FOR *H. melpomene* (SECOND SERIES). (1960).

All insects in this table are nonray (r)

Brood No.	♂ Parent			♀ Parent				Brood				
	Brood or Origin	Phenotype	Genotype	Brood or Origin	Phenotype	Genotype		BD	Bd	bD	bd	Total
1	"S" Surinam	Bd	?	"B" Surinam	?	?	♀	0	4	0	0	4
2	"D" Surinam	BD	bD/Bd	1	Bd	Bd/?d	♂	0	3	0	0	3
							♀	2	3	0	0	5
								2	6	0	0	8
3	32	BD	bD/Bd* or BD/Bd	2	BD	BD/Bd or bD/Bd*	♂	23	8	0	0	31
							♀	26	10	0	0	36
								49	18	0	0	67
4	17	BD	BbDd	3	BD	BbDd	♂	0	1	0	0	1
							♀	5	1	2	0	8
								5	2	2	0	9
5	3	BD	?	3	BD	?	♂	11	0	0	0	11
							♀	5	0	0	0	5
								16	0	0	0	16
6	3	BD	?D/Bd*	3	BD	?D/Bd*	♂	10	1	0	0	11
							♀	9	3	0	0	12
								19	4	0	0	23
7	3	Bd	Bd/Bd*	3	Bd	Bd/Bd*	♂	0	4	0	0	4
							♀	1	2	0	0	3
								2	7	0	0	9
8	"M" Surinam	Bd	Bd/bd	"E" Surinam	Bd	Bd/Bd	♂	0	25	0	0	25
							♀	0	17	0	0	17
								0	42	0	0	42
9	8	Bd	Bd/bd	8	Bd	Bd/bd	♂	0	2	0	1	3
							♀	0	1	0	0	1
								0	3	0	1	4
10	"M" Surinam	Bd	Bd/bd	"H" Surinam	Bd	Bd/bd	♂	0	10	0	1	11
							♀	0	10	0	2	12
								0	20	0	3	23

TABLE III. BREEDING DATA FOR *H. melpomene* (SECOND SERIES). (1960). (Continued)

All insects in this table are nonray (r)

Brood No.	♂ Parent Brood or Origin	♂ Phenotype	♂ Genotype	♀ Parent Brood or Origin	♀ Phenotype	♀ Genotype	Sex	BD	Bd	bD	bd	Total
11	10	bd	bd/bd	10	Bd	Bd/?d	♂	0	2	0	0	2
12	"Number 2" Trinidad	Bd	Bd/Bd	10	bd	bd/bd	♂	0	14	0	0	14
							♀	0	18	0	0	18
								0	32	0	0	32
13	9	bd	bd/bd	12	Bd	Bd/bd	♂	0	1	0	3	4
							♀	0	2	0	1	3
								0	3	0	4	7
14	"D" Surinam	BD	bD/Bd	"P" Surinam	Bd	Bd/Bd	♂	11	20	0	0	31
							♀	14	13	0	0	27
								25	33	0	0	58
15	14	BD	bD/Bd*	14	BD	bD/Bd*	♂	0	1	0	0	1
16	"Number 1" Trinidad	Bd	Bd/Bd	14	BD	bD/Bd*	♀	1	0	0	0	1
17	14	BD	bD/Bd	14	BD	bD/Bd	♂	1	0	0	0	1
							♀	3	1	5	0	9
								4	1	5	0	10
18	14	Bd	Bd/Bd*	14	BD	bD/Bd*	♂	1	0	0	0	1
19	14	Bd	Bd/Bd*	14	Bd	Bd/Bd*	♂	0	7	0	0	7
							♀	0	1	0	0	1
								0	8	0	0	8
20	14	Bd	Bd/Bd*	14	Bd	Bd/Bd*	♀	0	1	0	0	1
21	32	Bd	Bd/Bd*	14	Bd	Bd/Bd*	♂	0	36	0	0	36
							♀	0	35	0	0	35
								0	71	0	0	71
22	8	Bd	Bd/bd	14	BD	bD/Bd	♂	8	10	5	0	23
							♀	8	17	6	0	31
								16	27	11	0	54
23	8	Bd	Bd/bd	17	bD	bD/bD	♂	2	0	2	0	4
							♀	5	0	2	0	7
								7	0	4	0	11

TABLE III. Breeding Data for *H. melpomene* (Second Series). (1960). (Continued)

All insects in this table are nonray (r)

Brood No.	♂ Parent			♀ Parent				Brood				
	Brood or Origin	Phenotype	Genotype	Brood or Origin	Phenotype	Genotype		BD	Bd	bD	bd	Total
24	9	Bd	Bd/bd	17	bD	bD/Bd	♂	11	23	15	0	49
							♀	12	22	11	0	45
								23	45	26	0	94
25	19	Bd	Bd/Bd	17	bD	bD/bd	♂	1	4	0	0	5
							♀	1	0	0	0	1
								2	4	0	0	6
26	9	bd	bd/bd	17	bD	bD/bd	♂	0	0	14	8	22
							♀	0	0	13	9	22
								0	0	27	17	44
27	17	BD	BbDd	17	BD	BbDd	♂	4	4	1	0	9
							♀	0	2	1	0	3
								5	6	2	0	13
28	23	bD	bD/bd	23	bD	bD/bd	♂	0	1	2	1	4
							♀	0	0	5	1	6
								0	1	7	2	10
29	12	Bd	Bd/bd	23	bD	bD/bd	♂	2	3	0	3	8
							♀	4	7	2	5	18
								7	10	2	9	28
30	3	BD	BbDd	? Surinam Stock	BD	BbDd	♂	6	10	2	0	18
							♀	10	2	1	0	13
								16	12	3	0	31
31	32	Bd	Bd/Bd*	"Y" Trinidad	Bd	Bd/Bd	♂	0	32	0	0	32
							♀	0	23	0	0	23
								0	55	0	0	55
32	"D" Surinam	BD	bD/Bd	"Z" Trinidad	Bd	Bd/Bd	♂	3	3	0	0	6
							♀	1	1	0	0	2
								4	4	0	0	8

*Indicates that the genotype is not known for certain. The genotype given is the most probable, assuming that crossing over has not occurred. Words and letters within quotation marks are the designations of wild-caught butterflies. Discrepancies in the total numbers of offspring have been produced by insects which could not be scored for sex.

being *bD* and *Bd*). Again the amount of information is so small that no reliable estimate of the crossover value can be obtained.

From Tables II and III it will be seen that the following chromosomes, genotypes and phenotypes have been observed in our broods (not considering the *R* locus):

Chromosomes: *BD, bD, Bd* and *bd;*

Genotypes: *BD/Bd, Bd/Bd, bD/bD, Bd/bd, bD/bd, bD/Bd* and *bd/bd;*

Phenotypes: BD, bD, Bd and bd.

That is, all possible phenotypes and chromosomes occurred, and all but three of the possible combinations of those chromosomes. Taking the Ray pattern into account, the following phenotypes were found:

BDR, BDr, bDr, Bdr, bdr.

Other phenotypes have been found in the wild (Joicey & Kaye, 1916).

III. The Genetics of *H. erato*

A. Materials and Methods

Data presented by Beebe (1955) of broods reared from wild individuals of *H. erato* give information about the inheritance of various elements of the pattern in this species. The following symbols have been used in tabulating his results:—

B: a wide forewing band, as in *melpomene;*

Bᵇ: a complicated, broken forewing band, different from anything in the *melpomene* material;

D: red pigmentation of the base of the forewing, similar to that of Dennis in *melpomene*, but lacking the basal red on the hindwing;

d: absence of this red pigmentation;

R: Ray patterns, similar to those in *melpomene,* but extending into the basal area of the hindwing;

r: the absence of such red rays;

(y): indicates that the feature with which the symbol is bracketed is yellow instead of red; thus if B is a red forewing band, (By) is a yellow one;

w: presence of prominent white spots in the forewing band.

The difference between the Dennis and Ray patterns in the two species is worthy of special note and is illustrated in Text-fig. 1; for illustrations of the other patterns see the plates in Beebe's paper.

B. Results

Beebe's results are summarized in Table IV and permit the following conclusions:—

1. The female parent of Brood B, being from Trinidad where the species is monomorphic, must have been homozygous for all major wing-pattern loci. This means that in this brood the factors for the D pattern, R pattern and Bᵇ pattern (Broken-band) were all dominant and the male parent was homozygous. Unless complex factor interaction is involved, the gene for yellow coloring of the forewing band is recessive to the gene for red coloring.

2. It is therefore likely that brood D is a backcross for the *D* and *R* factors, the unknown male parent having been a heterozygote ($P > .5$). *D* and *R* could be recessive, as the fit to an F_2 ratio is also good ($P > .2$), but in view of the result for brood B this seems unlikely. The brood gives a strong suggestion of linkage between the *D* and *R* loci. Assuming that the brood is a double backcross, *P* for independent assortment is less than .001, and the maximum value for the crossover rate is 8% ± 7%. The data do not exclude the possibilities that (a) Dennis and Ray are pleiotropes of one gene, or (b) *D* and *R* are on separate chromosomes but that one can only express itself in the presence of the other; though both these alternatives seem unlikely because of the existence of specimens
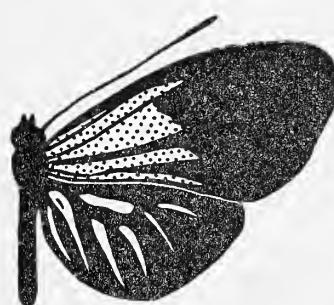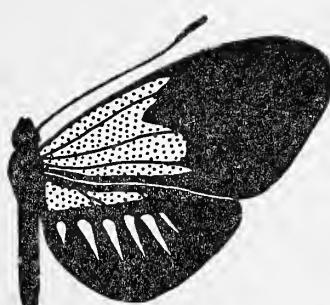
Text-fig. 1. Difference between Ray and Dennis elements in *H. melpomene* (left) and *H. erato* (right). Ray element white, Dennis element stippled.

TABLE IV. BREEDING DATA FOR *H. erato*.
(BEEBE'S DATA).

Brood Letter	♂ Parent Phenotype and Origin	♀ Parent Phenotype or Genotype and Origin	Brood					
			Bᵇ DR	Bᵇ DRw	(Bᵇy) Dr	BDR	Bdr	Total
A	? Surinam	BᵇDr Surinam	♀ 0	0	1	0	0	1
B	(Bᵇy)DR Surinam	*Bdr/Bdr* Trinidad	13	0	0	0	0	13
C	? Surinam	Bdr Surinam	♂ 1	0	0	0	0	1
			♀ 0	1	0	0	2	3
			1	1	0	0	2	4
D	? Surinam	Bdr Surinam	♂ 0	0	0	3	5	8
			♀ 0	0	0	2	3	5
			0	0	0	5	8	13
E	? Surinam	Bdr Surinam	♂ 0	0	0	0	2	2
			♀ 0	0	0	0	2	2
			0	0	0	0	4	4

Insects designated "?" were the wild mates of the females and were never seen.

in which Dennis occurs without Ray (vars. *dryope* and *cybelina;* see Seitz, 1913, Pl. 78) and in which Ray occurs without Dennis (var. *vesta;* see Seitz, 1913, p. 393).

3. Brood C therefore also provides evidence of linkage between the *D* and *R* loci, and between these two loci and the factor, apparently *Bᵇ,* which is affecting band-width in this brood; it is not possible to prove or estimate the linkage (*P* for independent assortment greater than .1). It is unlikely that the Bᵇ and D patterns are pleiotropes of the same gene, or appear linked because of factor interaction, as they can occur independently (vars. *callicopis* and *erythraea;* Seitz, 1913, Pl. 78).

4. Nothing can be said about the inheritance of white coloration.

5. There is no evidence for or against sex-linkage.

6. One reservation must be made: the apparent linkage of the various loci could have been produced even if the loci were not linked, if the females had mated twice in the wild; double matings have been suggested by Ford (1936) to explain anomalous broods reared from wild *Papilio* females.

IV. DISCUSSION

The polymorphisms of *Heliconius erato* and *H. melpomene* are of exceptional interest from a number of points of view. The species are undoubtedly aposematic (Crane and refs., 1955, preliminary observations; and L. P. Brower, J. V. Z. Brower & C. T. Collins, in prep., experi-mental study). Almost certainly the species are also Müllerian mimics and are involved in mimetic relationships of amazing complexity with numerous other Lepidoptera (Eltringham, 1916). Again, the hue red, which in the most usual form of both species is present as a forewing band, has high value in releasing courtship behavior; in fact an all-red model of about the size of a normal butterfly acts as a supernormal stimulus (Crane, 1955, on *H. erato* and in prep. on *H. melpomene.*) Finally, evidence is emerging (Beebe, Crane & Fleming, 1960; Alexander, 1960.1; and Crane *et al.* unpubl.) that *H. melpomene* and *H. erato* are closely related.

In those features studied so far, both polymorphisms are apparently controlled by loci in the same linkage group and are therefore polymorphisms of the type described by Sheppard (1953). At least two of the elements resulting in more extensive red markings than usual are dominant in both species, while that responsible for much reduced forewing bands is recessive.

We have emerging, therefore, in the study of these two species a number of related factors to be considered in our further examination of the biology and evolution of these and other heliconiines. First, the probable value of red as a warning hue associated with aposematism. Second, the definite value of the same hue in courtship behavior, additional amounts of red having, up to a certain size, extra stimulating value in experimental situations. Third, the dominance, as shown in the present contribution, of certain elements responsible for red in excess of the usual forewing band. Fourth, the apparent oc-

currence of polymorphic forms exhibiting more than a single red forewing area of moderate size in few geographic localities, compared with the wide distribution of the species. Fifth, our field observations (unpublished and incomplete) in Surinam, indicating that individuals with the larger areas of red markings are uncommon to rare in the field. Sixth, mimicry. Seventh, multilocus polymorphism with linked genes.

V. Summary

1. The butterflies *Heliconius melpomene* and *H. erato* are highly polymorphic; this paper, the first of two, describes differences produced by major genes.

2. In *H. melpomene* three major loci, all linked on the same autosome, have been discovered. They are:

B; affecting the width of the band on the forewing;

D: producing a red suffusion on the base of fore- and hindwing; and

R: producing red rays on the hindwing.

One of the crossover values appears to be low (less than 30%); the other has not been determined, although crossovers have occurred.

3. In *H. erato* the evidence is less certain but it seems that there are three loci, all linked, which produce patterns analogous to those produced by the three linked loci in *melpomene*. There are slight but important differences in the effects of D and R in the two species, and the B locus gene which narrows the band is dominant in *erato* but recessive in *melpomene*.

4. In *erato* there appears to be a single recessive factor which changes the color of the forewing band from red to yellow.

5. The interest of the polymorphisms in connection with courtship behavior, aposematism and linkage are noted.

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EXPLANATION OF THE PLATE

PLATE I

Specimens of *Heliconius melpomene* showing the major pattern elements discussed in this paper. All the butterflies are red and black, except that the diffuse C-shaped or triangular mark in the forewing cell of Figs. 3 and 5, and two small areas near the costal edge of the forewing of Fig. 3, are yellow; these yellow marks will be discussed in the second paper (Turner, 1962).

FIG. 1. Wide-band, Dennis, Ray (BDR).

FIG. 2. Wide-band, Dennis, nonray (BDr).

FIG. 3. Narrow-band, Dennis, nonray (bDr).

FIG. 4. Wide-band, nondennis, nonray (Bdr).

FIG. 5. Narrow-band, nondennis, nonray (bdr).

FIG. 1

FIG. 2

FIG. 3

FIG. 4

FIG. 5

THE GENETICS OF SOME POLYMORPHIC FORMS OF THE BUTTERFLIES HELICONIUS
MELPOMENE LINNAEUS AND H. ERATO LINNAEUS

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE

NEW YORK ZOOLOGICAL SOCIETY

Contents

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Effects of Hybridization on Pigmentation in Fishes of the Genus *Xiphophorus*

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(Plates I-VIII)

I. INTRODUCTION

THIS PAPER is dedicated to Myron Gordon. The dedication is particularly appropriate for a number of reasons. Most of the hybrids treated herein were produced under Dr. Gordon's direction, and publication of this work was one of many projects left unfinished by his untimely death in 1959. Dr. Gordon had caught the parental stock from which the crosses were made, founded the unique Genetics Laboratory of the New York Aquarium in which they were made and, most important of all, provided the rationale under which their existence and study assumed significance. It is especially fitting that the paper appears in the scientific journal of the New York Zoological Society; Dr. Gordon was intimately associated with the Society for the major part of his career and numerous scientific reports by him and his associates were published in *Zoologica* over the years. Finally, deep personal feelings add another dimension to the dedication. Myron Gordon was a dear friend as well as mentor. It was he who suggested the pigmentation of hybrids as a subject for a doctoral thesis and made available the fishes and facilities of the Genetics Laboratory.

Myron Gordon first recognized the remarkable combination of features that makes the fishes of the genus *Xiphophorus* so worthy of study (Atz & Rosen, 1959). Not the least of these is their ability to hybridize with one another. In fact, it was the melanotic hybrids of *X. maculatus—X. hellerii* that first brought these fishes to the attention of biologists and medical men (Atz, 1941). Because they have been more readily available for experimentation than the other species of *Xiphophorus*, because their hybrids often develop melanoma and because *X. maculatus* shows an unusual but clear-cut sex-linkage, these two species have been the subject of many more investigations than any of their congeners. Dr. Gordon's broad approach to the problems of comparative oncology, however, included a study of all the then known species of

Xiphophorus and their hybrids.[3] As can be seen in Table I, nearly two-thirds of the 28 crosses recorded up to the present were first made by Dr. Gordon (see the papers by Gordon, Gordon *et al.* and Rosen).

The author wishes to thank Dr. Donn E. Rosen for invaluable help received during many long and spirited discussions. Dr. Klaus D. Kallman, Research Associate in Genetics of the New York Aquarium, who succeeded Dr. Gordon in direction of the Genetics Laboratory, also provided valuable assistance, including a critical reading of the manuscript, and this is gratefully acknowledged. Special thanks are due the American Museum of Natural History, in particular the Department of Birds, for their most generous provision of space and facilities.

II. Materials and Methods

The hybrid fishes upon which this study is based have been produced over a period of more than 25 years, but the great majority of them are the result of crosses set up since 1939 in the Genetics Laboratory of the New York Aquarium. Almost all of the stocks of fishes that have been used were derived from specimens collected alive in their native Mexico or British Honduras, thus insuring purity of ancestry, for domesticated fish, obtained from pet stores or commercial breeders, almost invariably have a hybrid somewhere among their progenitors.

The following is a list of the strains used in the present studies, the geographical area from which they were taken, and the expedition responsible for collecting the foundation specimens:

Xiphophorus couchianus (Girard, 1859)[4]

Rio Santa Catarina, Nuevo Leon (1939) — Gordon, Atz, Evelyn Gordon; (1958)—Gordon, Evelyn Gordon.

Xiphophorus variatus xiphidium
(Gordon, 1932)

Rio Purificacion, Tamaulipas (1939)—Gordon, Atz, Evelyn Gordon.

Rio Santa Engracia, Tamaulipas (1958) — Gordon, Evelyn Gordon.

Xiphophorus variatus variatus (Meek, 1904)

Rio Axtla, San Luis Potosi (1939)—Gordon, Atz, Evelyn Gordon.

Xiphophorus variatus evelynae Rosen, 1960

Rio Necaxa, Puebla(1957)—Rosen, Malcolm Gordon, Gordon.

Xiphophorus montezumae montezumae
Jordan & Snyder, 1900

Rio Salto, San Luis Potosi (1957)— Rosen, Malcolm Gordon, Gordon.

Xiphophorus montezumae cortezi Rosen, 1960

Rio Axtla, San Luis Potosi (1939)— Gordon, Atz, Evelyn Gordon.

Xiphophorus pygmaeus pygmaeus
Hubbs & Gordon, 1943

Rio Axtla, San Luis Potosi (1940)— New York Aquarium Expedition to La Cueva Chica, C. M. Breder, Jr., leader.

Xiphophorus maculatus (Guenther, 1866)

8A—Domesticated, white, spotted strain (August 7, 1939)—Matsuno, New York, N. Y.

23 & 30 — Rio Jamapa, Veracruz (1939)— Gordon, Atz, Evelyn Gordon.

Gp—Rio Grijalva, Tabasco (1952)—Gordon.

Bp—Belize River, British Honduras (1949)— Gordon, Fairweather.

Xiphophorus hellerii strigatus Regan, 1907

3B — Arroyo Zacatispan, Oaxaca (1939)— Gordon, Atz, Evelyn Gordon.

124—Domesticated strain.

Xiphophorus hellerii guentheri
Jordon & Evermann, 1896

Gx—Rio Grijalva, Tabasco (1952)—Gordon.

Bx—Belize River, British Honduras (1949)— Gordon, Fairweather.

Xiphophorus hellerii

hx—Domesticated, albino strain.

A description of the laboratory in which these viviparous, tropical, freshwater fishes have been maintained and the care that is given them may be found in Gordon (1950c).

A total of 3,000 hybrids was involved in the present study. Most of the specimens were fixed and stored in formalin, some in ethyl alcohol. In addition to the hybrids, preserved examples of the strains from which they had been derived were examined, as well as numerous fish caught and preserved in the wild. The latter are now part of the collections of the Museum of Zool-

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[3] In accord with this approach, the recent discovery of two new species, *X. clemenciae* and *X. milleri,* and four new subspecies (Rosen, 1960) opens up a wide field of comparative genetics.

[4] With the exception of the spelling of *hellerii,* these scientific names are the same as the ones used by Rosen (1960) in his comprehensive revision of the teleost genus *Xiphophorus* (Family Poeciliidae, Order Cyprinodontiformes). The orthographic change is required by the International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology and published in 1961.

TABLE I. EARLIEST REFERENCES TO HYBRIDIZATION OF FISHES OF THE GENUS *Xiphophorus*[1]

Female	couchianus	variatus xiphidium	variatus variatus	Male maculatus	montezumae cortezi	pygmaeus pygmaeus	hellerii
couchianus	Rosen (1960) ●		Rosen (1960) ●	Gordon (1941)●	Kosswig (1959)		
variatus xiphidium			Nigrelli & Gordon (1951) Rosen (1960) ●	Kosswig (1935a) ●			
variatus variatus		Rosen (1960) ●		Bellamy (1936) Gordon & Smith (1938)		Gordon (1953) ●	Gordon (1941)[2]
maculatus	Gordon (1933) Reed, Gordon & Lansing (1933) Gordon & Smith (1938) ●	Gordon (1933) Kosswig (1935a) Gordon & Smith (1938) ●	Gordon (1933) Kosswig (1935a,b) Bellamy (1936) Gordon & Smith (1938) ●		Gordon (1941) Gordon (1951b)●	Gordon (1941) Gordon (1951b)[2]	Lösslein (1912)[3] Hafner (1912)[3]
montezumae cortezi	Rosen (1960) ●	Kosswig (1959) ●	Gordon (1953) ●	Gordon (1941) ●			
pygmaeus pygmaeus		Gordon (1941) ●	Gordon (1953) ●		Gordon (1953) ●		Kosswig (1936) ●
hellerii	Rosen (1960) ●	Kosswig (1935a, 1936)	Rust (1941) Gordon (1941)[2]	Gerschler (1914)[3] ●			

[1] The two or three subspecies of *X. hellerii* involved in various crosses have not been distinguished, partly because of the difficulty of identifying what form was used. Specimens of hybrids from the combinations marked with a dot (●) have been studied for this paper.

[2] No record or other evidence of this cross could be found in the Genetics Laboratory after the death of Dr. Myron Gordon.

[3] According to the historical review presented by Gordon (1931b).

ogy of the University of Michigan, Ann Arbor, Michigan (Rosen, 1960).

For practical reasons, we have had to confine our attention to patterns visible on the surface of the fish and also to melanic pigmentation, because the latter resists fading in ethyl alcohol, formaldehyde or glycerine — in contrast to the red patterns that occur in these fishes, for example. Two special techniques were used to facilitate the study of the morphology of pigment cells and patterns. Selected specimens were dehydrated in absolute alcohol and cleared in methyl salicylate (synthetic oil of wintergreen), as described by Gordon (1931a). The skins of others were dehydrated, cleared in xylene and mounted on slides in Permount.

The photographs of living and preserved fish were taken by Sam Dunton, Photographer of the New York Zoological Society, while those of cleared specimens and skins were made by Dr. Ross F. Nigrelli, Pathologist of the New York Aquarium.

III. Results

From both a genetic and morphological point of view, the pigmentary patterns of the fishes of the genus *Xiphophorus* may be divided into (1) those shared by all adult members of the form, or sometimes all adult members of one sex of the form, and (2) those found in some individuals but not in others. The latter comprise the polymorphic elements of the pigmentary system. They are made up of either micromelanophores or macromelanophores and are genetically controlled in most instances by single major genes. In contrast, the monomorphic or non-polymorphic patterns are composed of micromelanophores and scale melanophores and, as far as known, are controlled only by multiple genetic factors. Both types of pattern show variations that may be correlated to a greater or lesser extent with environment, age and sex.

The pigmentation of *Xiphophorus maculatus* has been described in detail by Gordon (1931a), and much of what he recorded also holds for the other members of the genus. Rosen (1960) has described the outstanding pigmentary features of all the species and subspecies, and a more detailed account of the forms under current discussion may be found in Atz (1959a). In *X. maculatus*, the patterns of macromelanophores are governed by major genes that are dominant and sex-linked, while the major genes that influence the polymorphic micromelanophore patterns are dominant and autosomal. Although the distinction between the two types of melanophores is definite, genetically speaking,

no diagnostic morphological features have ever been described. Macromelanophores are considerably larger than micromelanophores and may attain a diameter of 500 microns (Gordon, 1959), but the two types overlap in size. In practice, however, it is usually easy to distinguish between them because of the greater size and denser pigmentation of the macromelanophores.

1. Inheritance of Monomorphic Pigmentary Patterns in Hybrids.

That these pigment patterns are monomorphic precludes the use of most intraspecific crosses to analyze their genetic basis. Only mutants such as i for albinism or st for xanthism are available for genetic analysis. Interspecific or intraspecific hybridization provides, however, another means of revealing the hereditary foundation of species- or subspecies-specific characteristics. The individual genetic factors can seldom be identified, but the behavior of phenotypic characters or character-complexes may be studied, and from this conclusions may be drawn as to the nature of the genetic elements at work.

The many crosses between species and subspecies of *Xiphophorus* that were available made this type of analysis feasible. A series of pairs of opposing categories was set up (Tables II, III and IV) that represented pigmentary characters in which the parental species differed sufficiently to make the assignment of a hybrid to one or the other category, or to an "intermediate" one, not too arbitrary a procedure. Most of these fishes are partially covered by a pigmentary pattern that consists of parallel lines enclosing rhombic or hexagonal areas of lighter pigmentation. Superficially, this pattern appears to outline each scale, but its anatomical basis is formed by the scale pockets, each edge of which is bordered by a band of micromelanophores. This network has been appropriately called the *reticulum* by Rosen (1960), and it provides a natural basis for describing the patterns on the body since most of them, *e.g.* the *mid-lateral stripe,* can be considered as modifications of the reticulation (see Figs. 13, 18). *Vertical barring,* however, is clearly separable from the reticulum, lying deeper in the skin, as was pointed out by Gordon (1931a).[5] *Background pigmentation* and *inter-radial pigmentation* of the caudal fin are distinctive in *X. p. pygmaeus*, in which scale melanophores and skin

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[5] Gordon considered this pattern to consist of *parr marks,* but any resemblance or relationship it may have to the well-known salmonid pattern is problematical. For one thing, unlike the latter, it is frequently retained as the fish matures. See Fig. 18.

TABLE II. SUMMARY OF "DOMINANCE" RELATIONSHIPS AMONG NON-POLYMORPHIC
PIGMENTARY PATTERNS IN F_1 HYBRID *Xiphophorus*

	Total No. of Broods	Number of Broods:[1]		
		Inter-mediate	Resembling Female Parent	Resembling Male Parent
Reticulum				
Type	22	9	5	9
Extent	18	13	4	1
Mid-lateral				
Stripe	24	12	12	5
Background				
Pigmentation	4	0	1	3
Vertical Barring	22	18	5	3
Dorsal Fin Pattern	15	10	2	4
Caudal Fin Patterns				
Inter-radial				
Pigmentation	4	4	0	0
Caudal Edging	3	2	1	0
Ventral Edging	11	6	6	3
Dorsal Edging				
of Sword	3	1	0	3
Anal Fin, Caudal				
Edging	12	6	3	5
Mid-ventral Stripe	14	10	2	4
Deep-lying Spots	10	0	8	2
Totals	162	91	49	42

[1] Excess (20) above Total Number of Broods results from some broods having intermediate individuals
in addition to those resembling either male or female parent, and therefore being recorded in two columns.

melanophores (neither of which is associated with the reticulum and thus may be considered to belong to the background) are by far the most poorly developed, and in which pigmentation is lacking between the finrays of the tail. A thin, dark border along the caudal edge of the caudal fin is found in some male *X. p. pygmaeus,* and a somewhat similar pattern along the caudal edge of the anal fin in female *X. maculatus.* In the swordtails, there is a dark band of pigmentation that runs along the caudal peduncle as the *mid-ventral stripe* which may or may not extend onto the ventral edge of the caudal fin. The dorsal edge of the sword of male swordtails may also be edged in black, and the way in which this is accomplished differs in different species. *Deep-lying spots* are a unique pattern of *X. couchianus* and consist of groups of deep-lying pigment cells, apparently associated closely with blood vessels, some of which are nevertheless visible along the posterior flanks of the fish.

The following observations have been made from a study of the data from Atz (1959a), summarized in Tables II, III and IV:

(1) The F_1s are not always uniform, either within broods or among similar crosses—even when judged by the relatively coarse standards employed.

(2) Among the F_1s, about as many characters resemble those of either parental form as are intermediate.

(3) Although characters in certain F_1s may resemble the female parent, there is, in the aggregate, no sign of maternal influence, since F_1 characters as frequently resemble the male parent.

(4) The F_2s are more variable than the F_1s, but not so in the expression of all, or even a majority of the characters.

(5) Backcrossing tends to result in characters that resemble the parental species with which the hybrid was backcrossed, but this is not invariably the case.

(6) Nevertheless, the second backcross never fails to produce at least some individuals that resemble the backcross species in the character in question, and usually the ma-

TABLE III. COMPARISON OF VARIABILITY IN NON-POLYMORPHIC PIGMENTARY
PATTERNS BETWEEN F_2 AND F_1 HYBRID *Xiphophorus*

	Number of F_2 Broods Exhibiting:		
	No Increase in Variability	Increase Toward One Parental Form	Increase Toward Both Parental Forms
Reticulation			
Type	2	6	0
Extent	2	5	1
Mid-lateral Stripe	1	8	0
Background Pigmentation	1	1	0
Vertical Barring	3	5	0
Dorsal Fin Pattern	1	2	1
Caudal Fin Patterns			
Inter-radial Pigmentation	0	1	1
Caudal Edging	0	0	1
Ventral Edging	2	0	0
Dorsal Edging of Sword	2	0	0
Anal Fin, Caudal Edging	0	5	0
Mid-ventral Stripe	2	1	1
Deep-lying Spots	5	2	0
Totals	21	36	5

jority of the fish are practically indistinguishable from that species.

(7) A few characters, most notably ventral edging of the caudal fin, persist in some individuals after two backcrosses to the opposite parental species.

(8) Reciprocal crosses do not always produce similar offspring (*X. v. xiphidium* and *X. maculatus; X. m. cortezi* and *X. maculatus; X. h. guentheri* and *X. maculatus*).

(9) It seems impossible to predict, on any morphological basis, whether the expression of a given character will be "dominant," "recessive," or intermediate in the F_1.

(10) A character is occasionally "dominant" in one interspecific combination and "recessive" in another.

(11) Occasionally the expression of a character in the F_1 is noticeably different from that in either parent, sometimes resembling that of another species (Vertical bars like *X. v. xiphidium* in *X. couchianus* × *X. maculatus* and in *X. couchianus* × *X. v. variatus;* mid-lateral stripe like *X. v. variatus* in *X. h. strigatus* × *X. couchianus*).

2. Inheritance of Polymorphic Pigmentary Patterns in Hybrids.

The polymorphic pigmentary patterns of *Xiphophorus maculatus* have been extensively studied by Gordon and his collaborators, who have described them (Gordon, 1931a, 1948, 1951b; Gordon & Fraser, 1931), determined their mode of inheritance (Gordon, 1931b, 1937, 1947a, 1948, 1950a, 1956b), recorded and analyzed their frequencies in nature (Gordon, 1947a; Gordon & Gordon, 1957), and studied their development and physiology both in health and disease (Gordon, 1948, 1950a, 1951a,b, 1957, 1958a, 1959; Gordon & Smith, 1938; Nigrelli, Jakowska & Gordon, 1951). Similar, but not as extensive, studies have been made with five other species belonging to the genus *Xiphophorus*. Four of these are polymorphic, but only one, *X. variatus*, approaches the remarkable diversity of pigment patterns shown by *X. maculatus*.

a. Micromelanophore Polymorphic Patterns.

Many specimens of *X. maculatus, X. v. variatus* and *X. v. xiphidium* exhibit a distinctive arrangement of micromelanophores located on either side of the caudal peduncle at the base of the caudal fin and extending onto it in varying degrees. There are seven basic patterns in *X. maculatus* and four in *X. variatus*, some of which closely resemble each other. No fish ever carries more than two patterns, and genetic experiments

TABLE IV. EFFECTS OF BACKCROSSING ON NON-POLYMORPHIC PIGMENTARY
PATTERNS OF HYBRID *Xiphophorus*

	First Backcross			Second Backcross			Third Backcross	
	Total Number Broods	Broods Showing Change Toward B. C. Parent	Broods Resembling B. C. Parent[1]	Total Number Broods	Broods Showing Change Toward B. C. Parent	Broods Resembling B. C. Parent[1]	Total Number Broods	Broods Resembling B. C. Parent
Reticulation								
Type	12	8	10	10	1	10	2	2
Extent	10	9	7(3)	6	1	6		
Mid-lateral Stripe	12	10	9(2)	10	3	8(2)	2	2
Background								
Pigmentation	1	1						
Vertical Barring	7	4	3(2)	4	2	2(2)	2	2
Dorsal Fin Pattern	7	6	5(1)	7	1	7	2	2
Caudal Fin Patterns								
Inter-radial Pigmentation	1	1	1					
Caudal Edging	1	1	1					
Ventral Edging	6	6	2(4)	7	2	4(3)	2	2
Dorsal Edging of Sword	1			4	1	4	2	2
Anal Fin, Caudal Edging	7	5	1(5)	5	1	3(2)		
Mid-ventral Stripe	7	6	(5)	9	1	4(4)	2	2
Deep-lying Spots[2]	3	3	(3)					

[1] Numbers in parentheses represent broods in which not all individuals resemble the backcross parent, and these are not included in the other figures in the same column. The number of broods in this column often exceeds the number of broods that show a change toward the backcross parent, because some F1 hybrids already resemble the backcross parent in certain characters and many first backcross fish do.

[2] In one second backcross to *X. couchianus* (*X. maculatus* × *X. couchianus*), no deep-lying spots appeared, even though some of the first backcross fish had exhibited them.

have shown that each pattern is controlled by a member of a series of dominant, autosomal multiple alleles. Hybridization strongly indicates that the two series of alleles occupy the same locus in both species (Atz, 1959a). Two dominant, autosomal gene modifers that alter the appearance of the tail patterns in *X. maculatus* have been identified. One called *extensor* (E), changes the *comet* (Co) pattern, in which micro-melanophores form a thin, dark border along the dorsal and ventral edges of the caudal fin, into the *wagtail* complex, in which all the fins and certain other extremities are pigmented (Gordon, 1946). The other modifier (Cg) changes the *twin-spot* pattern (T) into a reversed, C-shaped pattern called the *Guatemala crescent* (Gordon, 1956). Gordon found that these modifier genes are present in at least some *X. hellerii*, and he indicated that this species was perhaps

their only source, the factors having entered the genome of various domesticated strains of *X. maculatus* by introgressive hybridization.

Evidence for the presence of an *extensor*-like gene in *X. v. xiphidium* was obtained in a brief series of crosses (Table V). A female *X. maculatus*, carrying the *comet* (Co) tail pattern, was mated to a male *X. v. xiphidium*, both parents being descended from wild-caught fish, and 51 of the 99 offspring showed *comet*. Of these, 14 had this pattern modified in the direction of the *wagtail* with an intensification and slight spread of the pattern itself, a darkening of part of each of the dorsal finrays and the appearance of heavy pigmentation on the upper and lower lips, the latter being a typical part of the *wagtail* complex (Fig. 1). When one of the hybrid females with this modified pattern was backcrossed to *X. v. xiphidium*, 30 of the offspring showed *comet* and

TABLE V.   INFLUENCE OF HYBRIDIZATION ON MICROMELANOPHORE TAIL
PATTERNS OF FISHES OF THE GENUS *Xiphophorus*

Factor	Parent with Pattern	Parent without Pattern	Modification of Pattern in Offspring	Cross[1]
Co	*maculatus* ♀	*xiphidium* ♂	Extension (slight *wagtail* effect) (see Fig. 1)	h20
Co	h20 ♀	*xiphidium* ♂	Enhanced *wagtail* effect (See Fig. 2)	h30
Co	h20 ♂	*xiphidium* × *variatus* ♀	Extension (slight *wagtail* effect)	h38
T	*maculatus* ♀	*guentheri* ♂	Extension (*Guatemala crescent*)	324
T	*maculatus* ♂	*cortezi* ♀	Extension (pseudo-crescent)	103B
O	*maculatus* ♀	*cortezi* ♂	Enhancement	80
Ct	*xiphidium* ♀	*variatus* ♂	Extension (pseudo-crescent) (see Fig. 7)	h4

[1] Number of cross, as designated in the records of the Genetics Laboratory of the New York Aquarium.

the 7 largest of these (at the time they were sacrificed) showed a more strongly expressed *wagtail,* with the caudal and dorsal finrays darkened for most of their length, the pectoral and anal finrays darkened to a lesser extent, and the lips heavily pigmented (Fig. 2). In contrast, when a hybrid male, showing a slightly developed *wagtail* pattern, was mated to a female intraspecific hybrid *X. v. xiphidium* × *X. v. variatus,* 57 of the offspring showed *comet* of which the 8 largest (at the time they were sacrificed) exhibited a *wagtail* pattern, better expressed than it had been among the members of the original hybrid cross, but not as strongly as it was among the backcross offspring just described. Gordon (1946) indicated that the *wagtail* pattern (CoE) was not apparent in young fish, but developed as they grew. This, however, cannot account for the absence of the *wagtail* effect in many of the Co fish, since some of these were adults when sacrificed and preserved. That the effect was enhanced by backcrossing to *X. v. xiphidium* indicates that more than one modifying gene was involved.

In a cross between a *twin-spot X. maculatus* and a swordtail from British Honduras, *X. hellerii guentheri,* all the hybrids that inherited T exhibited the *Guatemala crescent.* This pattern was compared, partly by means of cleared specimens, with some of the *Guatemala crescent* fish studied by Gordon (1956b). As far as the tail pattern was concerned, the fish appeared identical. In addition to the tail pattern, however,

there is a modification of pigmentation near the mouth of *Guatemala crescent* fish (Gordon, 1956b). Most prominent are two spots of heavy pigmentation at each mandibular junction. These were lacking in the present specimens; instead they showed a crescent of dense pigmentation immediately behind the upper lip, overlying the ethmoid region posteriorly and the heads of the premaxillae and maxillae anteriorly. The pigment was located in the dermis. An examination of *Guatemala crescent* fish in the collection of the Genetics Laboratory (which could not include all the specimens or crosses studied by Gordon) revealed that in only one other cross (250) did the TCg fish exhibit the crescent-shaped pigmented area behind the upper lip. The ancestry of the latter cross involved *X. maculatus* from both the Rio Jamapa and domestic sources and *X. hellerii strigatus* from the Rio Papaloapon. It thus revealed no obvious genetic relationship to the present cross.

Another modification of the *twin-spot* pattern occurred in hybrids of *X. m. cortezi* and *X. maculatus,* in which a shadowy, crescentic pattern was formed by micromelanophores more or less connecting the upper and lower spots. In the hybrids from another cross involving the same species, the *one-spot* tail pattern was larger than it ever appears in the parental species, *X. maculatus.*

The offspring of an intraspecific cross, involving a female *X. v. xiphidium,* and a male *X. v. variatus,* exhibited a complete range of tail pat-

terns from *cut-crescent* to *crescent*. (Fig. 7), although the *cut-crescent* of the female parent was entirely normal in appearance, and no *crescent*-bearing fish is known among the ancestors of the fish.

None of the offspring from the above crosses was bred, and so no information exists on the genetic behavior of their modified tail patterns; nor is there any other cross involving a fish carrying genes for the same tail patterns, which might indicate how widespread the supposed genetic modifiers may be.

b. Macromelanophore Polymorphic Patterns.

The patterns composed of macromelanophores are all polymorphic, that is, none of them occurs in every individual of the species. They can most simply be described as *spotted,* and the spots may be considered to vary from the size of single macromelanophores to broad bands of black pigment. Because of the relatively large size of macromelanophores and the concentration of melanin granules within them, these patterns appear darker and more sharply demarcated from their background than do the patterns composed of micromelanophores. Variation in location, size and number of spots is therefore readily apparent, and this circumstance may contribute significantly to the impression that the variability of the macromelanophore patterns is considerably greater than the variability of the micromelanophore ones. There is, however, no question about the greater range of expressivity of the major genes controlling macromelanophores in hybrid genomes, in which this may be increased to pathological melanosis on the one hand or reduced to no penetrance at all on the other (Gordon, 1951a).

Five basic macromelanophore patterns found in *X. maculatus* have been described by Gordon (1951b, pp. 175-179) and Gordon & Gordon (1957, pp. 3-6):

Spotted (Sp)—irregular spotting on sides.

Nigra (N)—irregular blotches or bands on sides.

Striped (Sr)—discrete rows of spots on sides.

Spotted dorsal (Sd) — irregular spotting on dorsal fin.

Spotted belly (Sb)—heavy spotting on belly and ventral and anal fins.

With rare exceptions, no more than two of these patterns occur in a fish, and there is good evidence that they are controlled by dominant, sex-linked alleles (Gordon, 1948). Crossing-over has occurred, however, so that two macromelanophore genes have become located on a single chromosome (MacIntyre, 1961). The

series might therefore better be designated as pseudoallelic.[6]

Gordon (1943) recognized a single macromelanophore pattern in *X. variatus* and in *X. xiphidium* (at that time considered to be separate species rather than subspecies as they are today), *viz., spotted* (Sp) but subsequent, unpublished, analysis revealed the presence of a second pattern, *spotted caudal*. Rosen (1960, p. 81), however, lists four macromelanophore patterns from *X. variatus, viz., spotted* (which he calls *blotched*), *spotted caudal, speckled* and *black-banded*. The latter three occur only in fish from the Rio Cazones, from which no living specimens have yet been collected for genetic studies. The *spotted* (Sp) pattern is inherited as a sex-linked dominant and, according to Atz (1959a), appears to be an allele of the Sp of *X. maculatus.*[7]

The *spotted* pattern in *X. variatus xiphidium* typically consists of numerous, somewhat diffuse spots located in the region of the mid-lateral line and immediately above it.[8] In size they approach, but never equal, the area of the exposed portion of a scale, but the great majority are considerably smaller, that is, less than half as large. As few as eight spots have been found on one side of a fish, but the number is usually very much more. A common variant of this pattern (in certain populations) is one in which the spots are so numerous that they form, at a distance, a band of pigmentation along the side of the fish. Closer examination reveals that this is composed of numerous closely grouped macromelanophores, many of them "touching" one another. Aside from a tendency to follow the reticular pattern (see below) and be concentrated near the mid-lateral line, however, no pattern can be discerned. Sometimes the distribution of macromelanophores is so generalized that the whole body of the fish above the region of the mid-lateral line appears flecked with pigment. In such fish, individual spots are hard to distinguish.

The majority of the larger spots in *X. v. xiphidium* are roundish, but the smaller ones take on less regular, more elongate forms. They usually appear more diffuse and less clearly defined than do the spots found on *X. montezumae cortezi,*

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[6] It was evidence and considerations of this nature that led Rosen (1960, pp. 76-77) to state that the macromelanophore genes "are not all members of a single allelic series."

[7] See Figs. 4-6 which show the P_1 and some of the F_1s of one of the crosses that revealed this relationship.

[8] See the P_1 male in Fig. 10 as an example of the appearance of Sp in this subspecies.

X. hellerii and, in some instances, *X. maculatus.* This may be the result of either or both of two factors: (1) as far as can be determined, the number of pigment cells per unit area of a spot is definitely less in *X. v. xiphidium* than in either *X. hellerii* or *X. montezumae,* and (2) there may be a lower concentration of pigment per cell in *X. v. xiphidium.* This could account for the differences observed between it and some strains of *X. maculatus,* where the number of cells appears to be substantially the same. A third possibility, of course, is that the macromelanophores are of different sizes, but those from the two swordtails appeared smaller, if anything, than those in *X. v. xiphidium.* This possibility could only be settled by treating live specimens with adrenaline to concentrate as uniformly as possible the pigment in the melanophores, fixing the fish in that state, and then making counts and measurements.

Although the *spotted* pattern of *X. v. xiphidium* is characterized by its variability and lack of definition, one feature always marks its distribution. This is its close spatial relationship to the reticulum; it is very rare that a spot or individual macromelanophore is found that does not seem to be touching or lying astride the reticulum — or is not occupying a place that would have shown reticulum, had it been present. In those cases, described above, where macromelanophores are so numerous that they practically form a horizontal band near the mid-lateral line, numerous cells must fall in areas between reticular elements, but this occurs only where the cells are so numerous that they "touch" or "overlap" one another. Even in these cases, the cells at the edges of the pigmented areas follow the reticulum.

The *spotted* (Sp) pattern of *X. variatus variatus* resembles that seen in *X. v. xiphidium* but differs in the following ways.[9] Typically the pattern is confined to the region of the mid-lateral line, but the spots are not concentrated in the latter region as frequently as they are in *X. v. xiphidium.* There are more large spots and no fish without large spots, except those from certain regions. There are numerous roundish spots, but because the spots sometimes follow the reticulum very closely, V- and Y-shaped ones are not rare. In some specimens from one region (Rio Tempoal), the spots so closely follow the reticulum that a pattern strongly reminiscent of the *striped* (Sr) pattern of *X. maculatus* is produced. Although the number of pigment cells per

unit area within a spot appears comparable to that in *X. v. xiphidium,* the intensity and sharpness of the spots is in general greater than in the latter subspecies. The range of variability of the *spotted* pattern is, however, greater in *X. v. variatus.*

Two macromelanophore patterns, *spotted* (Sp) and *spotted caudal* (Sc), are known in *X. montezumae cortezi* and each appears to be controlled by a single dominant, autosomal gene (Atz, 1959a). These are not alleles nor is Sc an allele of the Sp factor of *X. hellerii guentheri,* but no direct evidence exists concerning their relationship to the macromelanophore factors in other species. In *X. m. cortezi,* the *spotted* (Sp) pattern typically consists of prominent, deeply pigmented, roundish spots mostly confined to the mid- and post-dorsal regions, above the mid-lateral stripe, and to the dorsal and caudal fins. In size, individual spots approach, but rarely if ever exceed, the area of the exposed portion of a scale. Although there may be as few as five spots on one side of an adult-sized fish, there are usually many more. Analysis indicates that the number of spots increases with size, and presumably age, and that males exhibit more spots than females (Atz, 1959a). On the average, the closer one approaches the mid-dorsal line, the greater the density of spots (Fig. 13). The macromelanophores that comprise this pattern appear to be associated in some way with the reticulum, which is especially well developed in this species (Fig. 13). No spot was ever found that was not "touching" some part of the reticular pattern, that is, no spot was located entirely within the hexagonal or trapezoidal areas formed by the reticular elements. Usually the spots appeared to be directly astride the reticular bars and sometimes a halo effect was noticeable. In connection with the latter phenomenon, it should be noted that macromelanophores are located at or very near the same level in the dermis as are the micromelanophores. Another characteristic of the spots of *X. m. cortezi* is that they not infrequently coalesce, forming irregularly shaped blotches. On the dorsal fin, the spots are found in the interradial membranes, although they may extend over the finrays. In heavily spotted males, they tend to form two rows, one near the base of the fin, the other about halfway between base and distal edge. The spots on the dorsal fin are usually larger than those on the body. In females or immature fish, the *spotted* pattern rarely extends onto the dorsal fin. In some *spotted* males and a few females, there may be spots on the caudal fin as well. These are spindle-shaped or oval and generally small. They lie between or along the caudal finrays and have been seen to occur

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[9] See the *spotted* hybrids in Figs. 8 and 9 for unmodified examples of this pattern. Fig. 18 shows an enlargement of some macromelanophore spots from this subspecies.

between any two finrays except those involved in the sword. They seldom occur under the superficial caudal musculature at the base of the fin, but rather in the middle half of the exposed portion of the fin itself.

The tendency for macromelanophores to congregate in the caudal fin of *X. m. cortezi* is most strikingly seen in the *spotted caudal* (Sc) pattern. This consists of one or more irregular, elongate patches of heavy pigmentation, commencing close to the base of the caudal finrays and extending toward the rear for roughly one-third of the fin's length and ending in a variable number of irregular, tapering extensions of pigmentation (Fig. 15). These extensions usually are apposed to a finray; in fact, the whole pattern appears to develop in close relation to the caudal finrays. The macromelanophores invade the perimysia of the superficial muscle of the caudal fin as well as enveloping the finrays. In adult fish, the pattern may be only a sliver of pigmentation or it may be a blotch covering the second through the twelfth caudal finrays. Such large blotches are rare, however. Although the most frequent number of pigmentary patches comprising this pattern is one, two are not uncommon, and as many as four may be seen.

Macromelanophore spotting is known to occur in a small proportion of the individuals of two subspecies of *X. hellerii* (Rosen, 1960, pp. 120 and 126). In the form presently available, *X. h. guentheri,* genetic data indicate that the *spotted* (Sp) pattern is inherited as an autosomal dominant. Aberrant ratios have been noted, however, which might be explained by incomplete penetrance of Sp. It is noteworthy that true-breeding spotted *X. h. guentheri* were established in our Genetics Laboratory only after individuals exhibiting spots had been selected regularly to carry on the line for more than seven generations (Kallman, personal communication). Crosses with *X. maculatus* bearing Sr or Sd showed that these two factors are not alleles of the Sp from *X. h. guentheri* (Gordon, 1958b; Atz, 1959a). This pattern is notable for its relatively small number of large, intensely dark, irregularly shaped spots (Fig. 19). The irregularity is partly, but not wholly, the result of the coalescence of adjacent spots as a result of increase in size. Because of the discreteness of the spots, it is easy to study their morphology individually, and a series of stages beginning with a single macromelanophore and extending through intermediate stages (of, say, 30 macromelanophores) to large spots composed of uncountable numbers of pigment cells (in the order of hundreds but probably less than one thousand cells) could be distinguished. The most simple

explanation is that the spots increase in size through the appearance of more pigment cells. There is good evidence that the number of spots increases with the size of fish and therefore presumably with age (Atz, 1959a). The usual maximum size of a single spot, *i.e.,* one not involved in any coalescence with other spots, approaches the area of the exposed portion of a scale. Although the poor development of the reticulum makes the determination of relationship difficult, in all instances where such a determination could be made, the spots were seen to be closely associated with reticular elements. Frequently a halo effect is in evidence. The location of the spots on the body follows no discernible pattern save that they are much more frequently found on or above the mid-lateral stripe and somewhat more often in the pre- and mid-dorsal regions.

The effects of hybridization on macromelanophore patterns in 108 crosses are outlined in Table VI. The changes in the phenotypic expression of eight major genes belonging to five different species and subspecies vary from no discernible effect to loss of penetrance, on the one hand, and severe melanosis with the production of melanotic overgrowths, on the other. These results may be summarized by stating that they confirm and extend the conclusions reached by Gordon (1951b). The following are the observations resulting from an analysis of Table VI:

(1) Genes vary in their ability to respond to genetic influence from foreign genotypes. The gene for *spotting* (Sp) in *X. maculatus* is unquestionably the most potent in this respect; in no other species has it failed to produce well developed melanosis and, at least occasionally, neoplastic overgrowths in the form of melanomas (see items nos. 1-21 of Table VI). At the other extreme stand the genes for spotting in *X. hellerii guentheri* and *X. montezumae cortezi* whose expressivity changes to only a limited extent (nos. 82-91, 117-143) except in one hybrid combination (nos. 92-95).

(2) Species vary in their tendency to influence foreign genes controlling pigmentation. In *X. maculatus,* the species whose pigmentary genes are most capable of showing excessive growth in foreign genotypes, no enhancement of pigmentation belonging to patterns from other species has ever occurred (nos. 66-68, 78-80, 84, 98, 117-140). If any species could be assigned the role of being most likely to show melanosis and melanoma as a result of the introduction of foreign pigmentary genes into its genotype, *X. hellerii* would be the choice, based on its reactions to Sp, Sb, Sd and N (Gordon,

TABLE VI. INFLUENCE OF HYBRIDIZATION ON MACROMELANOPHORE PATTERNS OF FISHES OF THE GENUS *Xiphophorus*

No.	Parent with Pattern	Parent without Pattern	Offspring with Pattern[1]	Cross[2]
		Sp — X. maculatus		
1	*maculatus* ♂	*couchianus* ♀	F_1: Melanosis	h7
2	h7	h7	F_2: Severe melanosis to enhancement	h7[2]
3	*maculatus* ♀	*couchianus* ♂	F_1: Melanosis	h15
4	h15 ♀	*couchianus* ♂	BC: Melanosis (5) overgrowths (1)	91
5	h15 ♂♂♂	*couchianus* ♀♀♀	BC: Melanosis (4), severe melanosis (7), overgrowths (2)	92, 94, 99
6	99 ♂	*couchianus* ♀	2nd BC: Melanosis (6 out of 8)	100
7	91 ♀	*couchianus* ♂	2nd BC: Melanosis	101
8	*maculatus* ♀	*couchianus* ♂	F_1: Melanosis	845
9	845 ♀	845 ♂	F_2: Severe melanosis (2 out of 13) to moderate enhancement (6 out of 13); overgrowths (1 out of 13)	878
10	845 ♂	845 ♀	F_2: Severe mleanosis (2 out of 11) to moderate enhancement (2 out of 11)	880
11	845 ♀	*couchianus* ♂	BC: Severe melanosis	881
12	881 ♀	*couchianus* ♂	2nd BC: Severe melanosis	945
13	881 ♀	*couchianus* ♂	2nd BC: Severe melanosis	946
14	*maculatus* ♀	*couchianus* ♂	F_1: Severe melanosis	851
15	851 ♂	851 ♀	F_2: Severe melanosis (8) to melanosis (2)	893
16	851 ♂	*couchianus* ♀	BC: Severe melanosis (2); overgrowth (1)	934
17	*maculatus* × *variatus* ♂	*variatus* ♀	BC: Melanosis (3 out of 33); enhancement (see Figs. 4-6)	h61
18	*maculatus* ♂	*cortezi* ♀	F_1: Strong enhancement (9); melanosis (4); overgrowths (7)	103
19	*maculatus* ♂	*cortezi* ♀	F_1: Strong enhancement	103B
20	103	*cortezi*	BC: Melanosis (5); overgrowths (5)	103BC
21	h7 ♀	h3 ♂	Enhancement	h29
		Sd — X. maculatus		
22	*maculatus* ♂	*couchianus* ♀	F_1: Reduced penetrance	h7
23	*maculatus* ♂	*couchianus* ♀	F_1: Mild melanosis	325
24	*maculatus* ♀	*couchianus* ♂	F_1: No penetrance (14)	845
25	*maculatus* ♀	*couchianus* ♂	F_1: Melanosis	895
26	*maculatus* ♀	*xiphidium* ♂	F_1: Reduced penetrance (see Fig. 1)	h20
27	*maculatus* ♂	*xiphidium* ♀	F_1: No penetrance (see Fig. 3)	h31
28	*maculatus* ♀	320 ♂	BC: Mild melanosis; overgrowth (1)	350
29	*maculatus* × *strigatus* ♂	*guentheri* ♀	BC: Melanosis; overgrowths (2 out of 8)[3]	479
30	479 ♂	*guentheri* ♀	2nd BC: Severe melanosis (2); melanosis (6); enhancement (1); melanomas (4)[3]	671
31	479 ♀	*strigatus* ♂	2nd BC: Severe melanosis (1); melanosis (3); melanomas (2)[3]	672
32	h7 ♂	h2 ♀	No penetrance	h28
		Sr — X. maculatus		
33	*maculatus* ♂	*couchianus* ♀	F_1: No effect	68
34	68	68	F_2. Reduced penetrance and expressivity	68[2]

TABLE VI. INFLUENCE OF HYBRIDIZATION ON MACROMELANOPHORE PATTERNS
OF FISHES OF THE GENUS *Xiphophorus* (*Continued*)

No.	Parent with Pattern	Parent without Pattern	Offspring with Pattern[1]	Cross[2]
35	*maculatus* ♀	*couchianus* ♂	F_1: Enhancement	895
36	895 × 895		F_2: Mild melanosis (1), enhancement (6), reduced expressivity (3), strongly reduced expressivity (4)	895[2]
37	*maculatus* ♂	*xiphidium* ♀	F_1: Slight enhancement (see Fig. 3)	h31
38	*maculatus* ♂	h2 ♀	Reduced expressivity	h22
39	*maculatus* ♀	*cortezi* ♂	F_1: Slight suppression	h80
40	*maculatus* ♂	320 ♀	BC: Enhancement to nearly complete suppression (see Fig. 21)	384
41	*maculatus* ♀ × 384 ♂		2nd BC: Enhancement to nearly complete suppression	419
42	384 ♀	*maculatus* ♂	2nd BC: Reduced expressivity	486
43	486 ♀ × 486 ♂		No effect	523
44	486 ♀ × 486 ♂		No effect	524
45	486 ♀	486 ♂	No effect	525
46	*maculatus* ♂	320 ♀	BC: Slight enhancement	385
47	385 ♀	*maculatus* ♂	2nd BC: Reduced expressivity	421
48	421 ♂	*guentheri* ♀	Enhancement	458
49	458 ♀ × 458 ♂		Enhancement to nearly complete suppression	521
50	*maculatus* ♀	320 ♂	BC: Enhancement	386
51	*maculatus* ♀ × 386 ♂		2nd BC: Reduced expressivity	420
52	420 ♀ × 420 ♂		No effect to nearly complete suppression (see Fig. 22)	522
		$Sp - X.$ *variatus variatus*		
53	*variatus* ♂	*couchianus* ♀	F_1: No effect (see Fig. 8)	h23
54	*variatus* ♀	*couchianus* ♂	F_1: No effect	h13
55	h13 ♂	h13 ♀	F_2: No effect	h13[2]
56	*maculatus* × *variatus* ♂	*variatus* ♀	BC: No effect (see Figs. 4-6)	h61
57	*variatus* ♂	*cortezi* ♀	F_1: No effect (see Fig. 9)	h8
58	*variatus* ♀	*pygmaeus* ♂	F_1: Enhancement (1 out of 27) (see Fig. 11)	h1
59	*variatus* ♂	*pygmaeus* ♀	F_1: No effect	h11
60	h11	h11	F_2: No effect	h11[2]
61	*variatus* ♀	*xiphidium* ♂	F_1: No effect	h2
62	h2	h2	F_2: No effect	h2[2]
63	*variatus* ♂	*xiphidium* ♀	F_1: No effect	h3
64	h3	h3	F_2: No effect	h3[2]
65	*variatus* ♂	*xiphidium* ♀	F_1: No effect (see Fig. 7)	h4
66	h2 ♀	*maculatus* ♂	No effect	h22
67	h4 ♀	h20 ♂	No effect	h38
68	h2 ♀	h7 ♂	No effect	h28
		$Sp - X.$ *variatus xiphidium*		
69	*xiphidium* ♂	*cortezi* ♀	F_1: Strong enhancement (see Fig. 10)	903
70	*xiphidium* ♂	*cortezi* ♀	F_1: Strong enhancement	914
71	*cortezi* × (*cortezi* × *xiphidium*) ♂[4]	*cortezi* ♀	2nd BC: Severe melanosis with overgrowth (3)	941

TABLE VI. INFLUENCE OF HYBRIDIZATION ON MACROMELANOPHORE PATTERNS
OF FISHES OF THE GENUS *Xiphophorus* (*Continued*)

No.	Parent with Pattern	Parent without Pattern	Offspring with Pattern[1]	Cross[2]
72	*xiphidium* ♂	*pygmaeus* ♀	F₁:Mild melanosis (27 out of 28) (see Fig. 12)	h66
73	h66 ♀	*pygmaeus* ♂	BC: Enhanced melanosis (3 out of 9); reduced melanosis (2 out of 9)	106
74	*xiphidium* ♂	*evelynae* ♀	F₁: No effect	913
75	*xiphidium* ♂	*variatus* ♀	F₁ No effect	h2
76	h2	h2	F₂: No effect	h2²
77	*xiphidium* ♀	*variatus* ♂	F₁: Enhancement (see Fig. 7)	h4
78	*xiphidium* ♀	*maculatus* ♂	F₁: No effect (see Fig. 3)	h31
79	*xiphidium* ♂	*maculatus* ♀	F₁: Slight suppression to no effect (see Fig. 1)	h20
80	h20 ♀ × *xiphidium* ♂		F₁ & BC: No effect (see Fig. 2)	h30
81	h2 ♀	h7 ♂	Slight suppression	h28
		Sp — X. montezumae cortezi		
82	*cortezi* ♀	*couchianus* ♂	F₁: Reduced expressivity	849
83	*cortezi* ♀	*cortezi* × (*cortezi* × *xiphidium*) ♂[4]	2nd BC: Slightly reduced expressivity	941
84	*cortezi* ♂	*maculatus* ♀	F₁: No effect	h80
85	*cortezi* ♂	*pygmaeus* ♀	F₁: No effect	h12
86	h12	h12	F₂: No effect	h12²
87	*cortezi* ♀	*strigatus* ♂	F₁: No effect	h10
88	*cortezi* ♀	*strigatus* ♂	F₁:Reduced expressivity and penetrance (see Fig. 13)	h9
89	h9 ♂	*strigatus* ♀	BC: Slight suppression (see Fig. 14)	h27
90	h27 ♀ × h27 ♂		No enhancement	h27²
91	h27² ♀	*strigatus* ♂	Slight suppression	h39
92	*cortezi* ♂	*montezumae* ♀	F₁: No effect	900a
93	*cortezi* ♂	*montezumae* ♀	F₁: Enhancement (8 out of 11 ♂♂, 1 out of 12 ♀♀)	900b
94	*cortezi* ♂	*montezumae* ♀	F₁: No effect	900c
95	*cortezi* ♂	*montezumae* ♀	F₁: Strong enhancement (3 out of 9 ♀♀), enhancement (1 out of 9 ♀♀) (no Sp ♂♂ present)	900d
		Sc — X. montezumae cortezi		
96	*cortezi* ♀	*couchianus* ♂	F₁: No penetrance (3 adult, 16 immature)	849
97	*cortezi* ♀	*variatus* ♂	F₁: No penetrance (see Fig. 9)	h8
98	*cortezi* ♂	*maculatus* ♀	F₁: No penetrance	h80
99	*cortezi* ♀	*strigatus* ♂	F₁: Enhancement (see Fig. 15)	h26
100	h26 ♀	*cortezi* ♂	BC: Enhancement (2); no enhancement (1)	h40
101	h26 ♀	*strigatus* ♂	BC: Melanosis (1); enhancement (greater than in h40) (17)	h41
102	h41 ♀, h41 ♂	*strigatus* ♂, ♀	2nd BC: Enhancement (3); no enhancement (4)	h44, h45
103	h41 ♀	*strigatus* ♂	2nd BC: Severe melanosis (3); overgrowth (1); enhancement (16) (see Fig. 16) [3]	h42
104	h42	h42	Severe melanosis (2); overgrowths (5); melanosis to enhancement (31)	h42²

TABLE VI. INFLUENCE OF HYBRIDIZATION ON MACROMELANOPHORE PATTERNS
OF FISHES OF THE GENUS *Xiphophorus* (*Continued*)

No.	Parent with Pattern	Parent without Pattern	Offspring with Pattern[1]	Cross[2]
105	h42 ♀	*hellerii* (albino) ♂	3rd BC: Mild melanosis (3); overgrowths (2); enhancement (6)	h47
106	h42 ♀, h42 ♂	*strigatus* ♂ ♀	3rd BC: Severe melanosis (3); overgrowth (1); mild melanosis (2); enhancement (10); no effect (2)	h50
107	h50 ♀ × h50 ♂		Severe melanosis (2); overgrowths (5); enhancement (5); no enhancement (5)	353
108	h41 ♀ × h41 ♂		Enhancement	h43
109	h43 ♀ × h43 ♂		Melanosis (5); overgrowths (2;) enhancement (5)	h46
110	h46	h46	Severe melanosis (1); melanosis (5); overgrowth (1); enhancement (2)	h46[2]
111	h46[2]	h46[2]	Severe melanosis (1); enhancement (6); no enhancement (3)	h46[3]
112	h42[2] ♀	*hellerii* (*wagtail*) ♂	Overgrowth (1 out of 3)	314
113	*cortezi* ♂	*montezumae* ♀	F$_1$: Enhancement (6 out of 9 ♂♂, 1 out of 4 ♀♀)	900a
114	*cortezi* ♂	*montezumae* ♀	F$_1$: Enhancement (3 out of 11 ♂♂, 1 out of 8 ♀♀)	900b
115	*cortezi* ♂	*montezumae* ♀	F$_1$: Enhancement (3 out of 5 ♂♂, 2 out of 3 ♀♀), melanosis (2 out of 5 ♂♂)	900c
116	*cortezi* ♂	*montezumae* ♀	F$_1$: Strong enhancement (3 out of 11 ♀♀), enhancement (7 out of 11 ♀♀) (1 Sc ♂ present)	900d

Sp — X. hellerii guentheri

No.	Parent with Pattern	Parent without Pattern	Offspring with Pattern[1]	Cross[2]
117	*strigatus* × *guentheri* ♂	*maculatus* ♀	F$_1$: No effect	322
118	*guentheri* ♂	*maculatus* ♀	F$_1$: No effect (1)	324
119	*guentheri* ♀	*maculatus* ♂	F$_1$: No effect (see Fig. 20)	320
120	320	320	F$_2$: No effect	320[2]
121	320[2]	320[2]	F$_3$: Slight suppression	320[3]
122	320[3]	320[3]	F$_4$: Slight enhancement	320[4]
123	320 ♂	*maculatus* ♀	BC: Reduced penetrance and expressivity	350
124	320 ♂	*maculatus* ♀	BC: No effect	386
125	386 ♂	*maculatus* ♀	2nd BC: No effect	420
126	420 ♀	420 ♂	Slight enhancement (3 out of 35) (see Fig. 22)	522
127	320 ♀	*maculatus* ♂	BC: No effect (see Fig. 21)	384
128	384 ♂	*maculatus* ♀	2nd BC: Slight suppression	419
129	384 ♀	*maculatus* ♂	2nd BC: No effect	486
130	486 ♀	486 ♂	No effect	523
131	486 ♂	486 ♀	No effect	524
132	486 ♀ × 486 ♂		No effect	525
133	320 ♀	*maculatus* ♂	BC: No effect	385
134	385 ♀	*maculatus* ♂	2nd BC: Reduced expressivity	421
135	421 ♀	*guentheri* ♂	No effect	485
136	421 ♂	*guentheri* ♀	No effect	458

TABLE VI. INFLUENCE OF HYBRIDIZATION ON MACROMELANOPHORE PATTERNS
OF FISHES OF THE GENUS *Xiphophorus* (*Continued*)

No.	Parent with Pattern	Parent without Pattern	Offspring with Pattern[1]	Cross[2]
137	458 ♀	458 ♂	No effect	521
138	*guentheri* ♀	*maculatus* × *strigatus* ♂	BC: Slight enhancement (1 out of 8) [5]	479
139	479 ♂	*guentheri* ♀	2nd BC: No effect [5]	671
140	479 ♀	*strigatus* ♂	2nd BC: Slight suppression [5]	672
141	*guentheri* ♂	*strigatus* ♀	No effect	321
142	*guentheri* × (B.C. and inbred, ScCoE, *hellerii-cortezi* hybrid ♂	*strigatus* ♀	No effect	751
143	751 ♂	*strigatus* ♀	BC: No effect	887

[1] Described by means of a somewhat arbitrary series of classes, ranging from complete absence of macromelanophore pattern to melanoma, all but the first two categories being concerned with expressivity:

No penetrance   Enhancement
Reduced penetrance   Strong enhancement
Nearly complete suppression   Mild melanosis
Reduced expressivity   Melanosis
Slight suppression   Severe melanosis
No effect (*i.e.*, normal)   Overgrowths (melanoma)
Slight enhancement

Numbers in parentheses indicate the number of fish

[2] Number of cross as designated in the records of the Genetics Laboratory of the New York Aquarium. When more than one macromelanophore pattern was involved, the cross has been listed under each genetic factor.

[3] Photographs of other melanotic members of h42 may be found in Gordon (1951b, p. 199) and as Fig. 1 of Marcus & Gordon (Zoologica, 39: 123-131, 1954). The caption of the latter erroneously implies that the fish belong to h50.

[4] Fish received in 1958 from Dr. Curt Kosswig (see Kosswig (1959) for a general account of the genetic background of this fish).

[5] In designating backcrosses (BC), *X. hellerii strigatus* and *X. hellerii guentheri* have been equated.

1948, and nos. 28-31) and Sc (nos. 99, 101-112).

(3) The same gene may vary both positively and negatively under the influence of different genomes. Sd may show reduced penetrance or none at all (Gordon, 1951a and nos. 22, 24, 26, 27, 32) or melanosis with melanoma (Gordon, 1951a and nos. 23, 25, 28-31). Similarly Sr exhibits both reduced and enhanced expressivity (Gordon, 1948 and compare nos. 33-34, 38, 39 with 35, 36, 37), while Sc varies in expression from no penetrance to severe melanosis and melanoma (compare nos. 96-98 with 99-112).

(4) Crosses involving the same pigment patterns and species sometimes give different results (compare nos. 1, 3 and 8 with 14; 40 with 46 and 50; 41 with 42; 87 with 88; 92 and 94 with 93 and 95; 102 with 103; 123 with 124, 127 and 133). This probably indicates that several genes and their alleles are involved in the modification of the pig-

mentary patterns and that different combinations of these are present in different individuals.[10]

(5) Backcrossing to the parental form from which the macromelanophore pattern originated lessens the enhancing or reducing effect of hybridization on its expression (compare nos. 40 with 42, 46 with 47, 50 with 51, 99 with 100 and 101). Gordon & Smith (1938) backcrossed a melanotic F_1 hybrid, *X. maculatus* × *X. variatus xiphidium*, to *X. maculatus* and obtained fish

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[10] The age at which the fish were sacrificed is a variable that was controlled only in a general way, and this undoubtedly is the reason for some of the varied results. In the examples given above, however, the broods were of roughly the same age or the differences were so striking that ontogenetic stage could not account for them. At any rate, these crosses serve as a salutary warning against dogmatic assertions unless they are backed up by a replication involving several of the same crosses made with fish from different genetic strains.

with no melanosis, and Kosswig (1948) reported results of a similar nature.

(6) Backcrossing to the parental form that did not carry the macromelanophore pattern increases the enhancing or reducing effect of hybridization on its expression (compare nos. 4 and 5 with 3, 11 with 8, 73 with 72, 101 with 99). A plateau is soon reached, however, and further backcrossing may even result in a diminution of the effect (compare nos. 6 with 5, 7 with 4, 12 and 13 with 11, 20 with 18, 102 with 101, 105 and 106 with 102 and 103).

(7) Inbreeding frequently increases the range of phenotypic expression of macromelanophore patterns (compare 2 with 1, 9 and 10 with 8, 34 with 33, 36 with 35, 49 with 48). Two series of successive inbreedings showed variability in the average expression of the pigmentary pattern, the mean or mode of expression not necessarily being the same for successive generations (nos. 108-111 and 120-122). Gordon & Smith (1938) also obtained more variable F_2 offspring in two crosses of *X. maculatus* × *X. couchianus* and one of *X. maculatus* × *X. variatus xiphidium*.

(8) The same individuals may show enhancement of one macromelanophore pattern and no change or reduction in the expressivity of another (compare nos. 28 and 123, 30 and 139, 31 and 140, 26 and 79, 40 and 127, 48 and 136, 49 and 137, 50 and 124, 57 and 97, 71 and 83, 92 and 113, 94 and 115).[11]

IV. DISCUSSION

1. Genetics of Micromelanophore Pigmentary Patterns as Revealed by their Appearance in Hybrids.

The behavior of the reticulum and other non-polymorphic micromelanophore patterns in interspecific crosses within the genus *Xiphophorus* strongly indicates that their inheritance is controlled by polygenes, that is, by relatively numerous factors, each of which has a small phenotypic effect. This is in accord with the conclusions reached by Kosswig (1948) and with analyses indicating the type and number of genes involved in the species differences of other kinds of animals (Dobzhansky, 1937). The intermediate appearance of the F_1, the more variable F_2, and the return in appearance toward successive backcross parents are all classical indications of

polygenic inheritance. In none of these ways, however, did the present hybrids perform entirely in the classical manner; in fact, unorthodox responses were sometimes as much in evidence as classical ones. For example, approximately the same number of characters in the F_1 resemble either parent as are intermediate (see Table II and discussion on p. 176). Although the classical genetic behavior of the present hybrids would be hard to explain except on the basis of polygenes, the failure to conform to the above criteria does not indicate the converse. The appearance of unstable developmental systems as a result of the mixing of two foreign, mutually unadapted genotypes (Schmalhausen, 1949; Lerner, 1954) could very well bring about seemingly inconsistent results. Such a reduction in genetic homeostasis, as Lerner has designated it, could also account for the striking lack of uniformity occasionally seen in F_1 broods in which these hybrids were as variable as the F_2 broods arising from them, or even more so. Gordon & Rosen (1951) also found high variability in two gonopodial characters of F_1 hybrids between *X. maculatus* and *X. hellerii*. It is of interest to note that Hubbs & Strawn (1957) have warned that high variability in a population of fish is not a safe criterion for hybrid fertility, that is, for the presence of F_2, F_3 ... F_n generations, because high variability is sometimes exhibited by the F_1—which may be sterile. Hubbs (1956) attributed this variability to the combination of dissimilar developmental rates of the parental forms, and this may be considered a special case of the more general phenomenon of genetic homeostasis mentioned above.

Genetic modification of the polymorphic tail patterns has been an accepted but meagerly documented part of the concept of hereditary influences on pigmentation in fishes of the genus *Xiphophorus*. Hybridization has served to reveal additional examples of this phenomenon. Although the presence or absence of each polymorphic pigmentary pattern is typically controlled by a single gene, numerous other genes undoubtedly influence its phenotypic expression. The problem of identifying genic modifiers, the vast majority of which have small *plus* or *minus* effects, is at present insurmountable. The specific effects of two modifications of the tail patterns of *X. maculatus* have, however, been described by Gordon and attributed to two dominant, non-allelic genes. Similar modifications have appeared in the tail patterns of a few of the present interspecific hybrids (Table V).

On one occasion the *wagtail* effect was observed when a female *X. maculatus* carrying the

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[11] Gordon (1958b) briefly reported on the first three crosses listed here.

comet (Co) pattern was crossed with *X. v. xiphidium*. Gordon (1946) showed that this *extensor* effect, in which supplementary pigmentation appears around almost all of the finrays, the mouth and the operculi, results from the presence of a single dominant autosomal gene (E) that does not belong to the series of multiple alleles affecting tail patterns of which *comet* is a member. He also showed that this factor was present in *X. hellerii*. Whether the same factor is present in *X. v. xiphidium* is problematical, however, since the *wagtail* pattern is much more variably and also less clearly expressed in the *maculatus–xiphidium* hybrids than in the interspecific crosses in which Gordon was able to demonstrate the presence of E. Moreover, backcrossing to *X. v. xiphidium* heightened the expressivity of the *wagtail* pattern, an effect not seen in Gordon's fish, since the pattern appeared in the F₁ full-blown, so to speak. At the very least, however, we may conclude that in some individuals of *X. v. xiphidium,* there are genes capable of modifying the *comet* pattern of *X. maculatus.*

Gordon (1956b) described the modification of the *twin-spot* (T) pattern of *X. maculatus* to form the *Guatemala crescent,* and he presented genetic evidence that a dominant, autosomal, independently segregating gene is responsible, which he designated Cg. He indicated that this gene was probably present in an appreciable number of *X. hellerii.* This pattern appeared, but in a slightly modified form, when a *twin-spot X. maculatus* was crossed with *X. hellerii guentheri.* This modification may be the result of additional modifying factors or may represent the phenotypic expression of an allele of Cg. Another modification of the *twin-spot* pattern of *X. maculatus* appeared in a cross with *X. montezumae cortezi.* The extension of pigment was, however, less definite than in the *Guatemala crescent* and was not associated with any extra pigmentation around the mouth. With regard to other possible modifications of tail patterns in hybrids involving *X. montezumae cortezi,* it might be mentioned that in a cross with a *one-spot* (O) *X. maculatus,* this pattern was exceedingly intense. The puzzling relationship of *crescent* (C) to *cut-crescent* (Ct) shown in one cross between two subspecies of *X. variatus* could only be elucidated by further crosses. It does serve to emphasize, however, the similarity of the developmental processes involved in the two patterns.

2. *Genetics of Melanosis and Melanoma in Hybrids.*

The striking exaggeration of expression that

certain macromelanophore patterns exhibit under the influence of foreign genotypes has attracted more attention than any other feature of the genetics of *Xiphophorus.* Gordon (1951b, 1957) has reviewed the extensive experiments performed with *X. maculatus, X. hellerii* and their hybrids and summarized the concepts that have been developed from them. Crosses involving these and other members of the genus in new combinations have yielded results that are most easily interpreted in the same way. They therefore add to the confidence with which we may accept the concepts developed by Gordon over the years.

a. *Capacity for Atypical Growth and Specificity of Macromelanophore Genes.*

Gordon (1948) pointed out that the different macromelanophore patterns of *X. maculatus* are enhanced to different degrees in hybrids with *X. hellerii,* and Gordon & Smith (1938) and Gordon (1951b) showed that the same pattern, *viz.* the *spotted* pattern of *X. maculatus,* is enhanced to different degrees in hybrids with different species. The same relationships hold for the macromelanophore patterns of species other than *X. maculatus* (Table VII). On the basis of present work and that of Gordon (1948, 1951b), the allelic series of sex-linked dominants may be arranged according to their potency for melanosis and melanoma production in hybrid combinations:

     Sp (spotted) *X. maculatus*

     Sb (spotted belly) *X. maculatus*

     N (nigra or black-sided) *X. maculatus*

     Sd (spotted dorsal) *X. maculatus*

     Sr (striped) *X. maculatus*

     Sp (spotted) *X. variatus xiphidium*

     Sp (spotted) *X. variatus variatus*

The specificity that these genes exhibit in their morphological manifestations must, of course, be the product of equally specific physiological processes, and these genetically controlled events maintain a definite measure of specificity under the abnormal conditions imposed by hybridization, even though the limits of their phenotypic variability may be considerably increased. It is to be noted, for example, that certain hybrids in which two major macromelanophore genes are present show one pigmentary pattern in an enhanced form while the other remains within normal limits or even suffers some loss in expressivity (Table VI, and item 8 on p. 169). One of the reasons for the series of backcrosses and inbreedings conducted with the offspring of the cross of a spotted *X. hellerii guentheri* with *X. maculatus* (Table VI, nos. 119, 133-137) was

TABLE VII. MACROMELANOPHORE GENES OF FISHES OF THE GENUS *Xiphophorus* RANKED ACCORDING TO THEIR CAPACITY FOR ATYPICAL GROWTH IN HYBRIDS[1]

Factor	Species	Location of Spotting	Capacity for Atypical Growth	Mode of Inheritance	Relation to Other Genes
Spotted (Sp)	*X. maculatus*	Body and tail	Melanomas in some F₁ combinations and all backcross combinations[2]	Sex-linked dominant	Allelic
Spotted Dorsal (Sd)	*X. maculatus*	Dorsal fin	Melanomas in some F₁ and backcross combinations[2]	Sex-linked dominant	Allelic
Striped (Sr)	*X. maculatus*	Body and tail	Melanomas in one backcross combination[2]	Sex-linked dominant	Allelic
Spotted (Sp)	*X. variatus xiphidium*	Body and tail	Melanomas in one 2nd backcross combination; mild melanosis in two F₁ combinations[2]	Sex-linked dominant	Allelic
Spotted Caudal (Sc)	*X. montezumae cortezi*	Caudal fin	Melanomas in one 2nd backcross combination; strong enhancement in two F₁ combinations[2]	Autosomal dominant	Non-allelic[4]
Spotted (Sp)	*X. montezumae cortezi*	Body, tail, dorsal and caudal fins	Strong enhancement in one F₁ combination	Autosomal dominant	Non-allelic[4]
Spotted (Sp)	*X. variatus variatus*	Body and tail	Enhancement in one F₁ combination[3]	Sex-linked dominant	Allelic
Spotted (Sp)	*X. hellerii guentheri*	Body and tail	None	Autosomal dominant	Non-allelic[4]

[1] Based on Gordon (1948, 1951b) and data from Table VI.

[2] Backcross combinations refer only to backcrosses to the species or subspecies from which the macromelanophore pattern did not originate.

[3] Enhancement exhibited by a single fish out of a total of more than 200 hybrids. Kosswig (1937) states that the dominant, sex-linked gene P of *X. v. variatus* (probably identical with Sp) is responsible for spots that are more weakly expressed in hybrids with *X. hellerii* than they are in the parental species, but more strongly than they are in hybrids with *X. maculatus*. As far as crosses with *X. hellerii* were concerned, this observation was based on tri-hybrids produced by Kosswig (1935a, b) in which *X. maculatus*–*X. hellerii* hybrids were crossed with *X. v. variatus*. Rust (1941) notes that the spots of P are formed by macromelanophores. His illustration of a spotted hybrid from the cross, *X. hellerii* ♀ × *X. v. variatus* (P) ♂ shows no enhancement of this pattern. Rust also describes the inheritance of a dominant, sex-linked gene O of *X. v. variatus*, which is expressed as black spots on a light orange background. According to Kosswig (1948), this factor gives rise to tumors when introduced into the *hellerii* genome. Rust does not mention any pigmentary abnormalities in his paper, but he illustrates two O-bearing fish, the offspring of second backcrosses to *X. hellerii*, that show signs of a dark, pigmented overgrowth in the region near the base of the sword. Unfortunately, all fish carrying the O gene were lost during World War II (Kosswig, *in litt.*).

[4] None of these genetic factors appears to be allelic; as far as known they occupy non-homologous chromosomes.

to test what might for convenience be called the integrity of the Sp gene. The rationale was to introduce the gene into the *X. maculatus* genotype by the appropriate cross, followed by several backcrosses to *X. maculatus*. Reintroducing the gene into *X. h. guentheri* would reveal a modification of it (through the acquisition of gene modifiers or some change in the gene itself) in the form of enhanced expressivity. Inbreeding at various stages in the process would serve to increase the variability of genetic combinations and bring out latent factor interaction. The anticipated negative results were obtained in full measure; no change could be detected.

On the other hand, the fact that *X. maculatus*, the species in which the most potent melanosis- and melanoma-producing genes occur, has never been known to give rise to hybrids exhibiting any enhancement of patterns from other species (Table VI, nos. 79, 84, 98, 119) points to some similarity in physiological process underlying the actions of all the macromelanophore genes (Atz, 1959b). According to Gordon's hypothesis of the integration of macromelanophore genes into the genotype of *X. maculatus* (see p. 173), this species possesses several modifying genes that control the growth of its own macromelanophores. Presumably this control is general enough to exercise restraint on macromelanophore genes from other species, and this in turn presupposes some similarity in the biochemical processes of the genes being regulated. The existence of species like *X. hellerii*, the hybrids of which seem to be especially likely to exhibit enhanced pigmentary patterns, similarity provides support for the idea of biochemical characteristics common to all macromelanophore genes; but the fact that the hybrids of *X. couchianus* and *X. p. pygmaeus*, both of which lack macromelanophore patterns, do not show as great a degree of atypical macromelanophore growth as do those of *X. hellerii* and *X. m. cortezi*, which do have such patterns, indicates important differences between the macromelanophores of *X. maculatus* and *X. variatus* on the one hand and those of *X. hellerii* and *X. m. cortezi* on the other. Evidently the ability of the latter two species to control the growth of their own macromelanophore patterns confers little or no ability to control the growth of others. Of less critical value is the observation that the manifestations of atypical growth shown by the macromelanophores from different species appear to be basically the same. In all known hybrid combinations, melanosis necessarily precedes melanoma. Reed, Gordon & Lansing (1933) and Gordon & Smith (1938) have described several characteristics in which the mel-

anoses and melanomas of *maculatus-couchianus* hybrids resemble those of the more completely described *maculatus-hellerii* ones, and Gordon & Nigrelli (1949) stated that the melanomas found in *cortezi-hellerii* hybrids are histologically not unlike those found in other combinations.

Anders *et al.* (1961, 1962) have reported that the amount of free amino acids in various species of *Xiphophorus* varies inversely with the ability of their macromelanophores to produce tumors in hybrids: *X. maculatus* has the smallest quantity, *X. variatus xiphidium* a greater amount, *X. montezumae cortezi* still more and *X. hellerii guentheri* the greatest. This is the order in which the authors rank the species according to the potency of their macromelanophores for atypical growth in various hybrid combinations, *X. maculatus* having the most potent genetic factors and *X. hellerii* the least. This arrangement agrees substantially with the one in Table VII, which is based on independently acquired data. The significance of the apparent relationship between tumor production or susceptibility and amino acids has yet to be explained.

b. Evidence for the Evolution of Macromelanophore Genes and Their Polygenic Modifiers.

The tendency for increased variability in the F_2, the return toward the parental type in one backcross and the exaggeration of the modifying effect in the other are all most easily accounted for by assuming the presence of several modifying factors, as Kosswig (1931) did in order to explain similar findings involving *X. hellerii* and *X. maculatus*. Kosswig and Gordon (1937) explained their results with these two species on the basis of a few, perhaps only two, pairs of modifiers. The similarity of results between the present crosses and theirs, particularly the rapidity with which a plateau of enhancement is reached with repeated backcrosses to the P_1 carrying the modifying genes, indicates that approximately the same number of modifiers is involved in the presently studied species interactions.

Gordon (1950b, 1951b, 1958a), and Gordon & Gordon (1957) considered the production of melanosis and melanoma in *Xiphophorus* hybrids from an evolutionary point of view. They described how the combination of a potentially harmful gene, like Sp, and a series of modifying genes that render it harmless might have arisen. When the mutation to Sp first occurred, it is supposed to have been detrimental in a manner similar to the way Sp leads to melanosis and melanoma when introduced into foreign gen-

omes today.[12] Fisher (1928) and others have shown that such a gene, whose over-all effect is deleterious, will accumulate genic modifiers that tend to make the expression of its harmful effects recessive and, sometimes, eventually mask them completely—providing that the locus in question continues to yield mutant genes of the type upon which natural selection can operate. If this has indeed been the history of the integration of macromelanophore genes into the genotype of *X. maculatus,* the genotypes of the other species belonging to the genus *Xiphophorus* might better be considered to lack the genes or alleles that control the expression of the macromelanophore gene, rather than to possess genes that enhance its expression, as postulated by Kosswig(1931), or to remove a specific inhibitor that controls its normal growth and multiplication, as suggested by Gordon & Smith (1938). This clarifying view, which represents more than just a change in the terminology used to describe the interacting genomes, was suggested in 1958 by Donn E. Rosen, who was then a member of the staff of the Genetics Laboratory of the New York Aquarium.

Gordon (1951a, b, 1957) showed that the same kinds of abnormalities in the development of pigment patterns occur in intraspecific hybrids as do in interspecific ones, although they are not as strongly expressed. He considered this to be good evidence that subspecies and other geographically isolated populations of *Xiphophorus* are proceeding along paths of genetic differentiation similar to those already taken by the species. In a small series of crosses between the two subspecies of *X. montezumae,* two macromelanophore patterns from one of them were enhanced to an abnormal degree (Table VI, nos. 93, 95, 113-116). This provides another example of incipient melanosis, presumably the result of the mixing of different constellations of modifying genes that have evolved at the subspecific level of genetic differentiation.

In evaluating the significance of the pigment cell abnormalities of hybrids as a criterion of taxonomic relationship, Rosen (1960) pointed out that the degree of abnormality could act as a measure of the degree of genetic difference and should, therefore, enter into the determination of

systematic relationship. He indicated, however, that the correlation between the relative taxonomic position (as determined by a whole array of pertinent data) of any two non-interbreeding groups (species, subspecies or merely river-system populations) and the hybrid pigmentary abnormality exhibited by their hybrids is far from perfect. The present data support this view. For example, intraspecific crosses, between subspecies, may or may not result in offspring with atypical macromelanophore patterns (Table VI, nos. 61-65, 74, 75-77, 92-95, 113-116, 141). In interspecific crosses, the same macromelanophore gene may lead to an enhanced pattern in some combinations or a normal pattern, or none at all (zero penetrance) in others (Table VI, compare 69, 70, 71 with 78 and 79; 99 with 97, 98). Moreover, in the same interspecific cross, one pattern may be enhanced and another unaffected or reduced in expressivity (Table VI, compare 18 and 19 with 98; 99 with 87 and 88). It is nevertheless true that pigmentary abnormalities in interspecific hybrids are more severe and more frequently encountered than in intraspecific ones, as Gordon (1951b) and Rosen (1960) have indicated. Yet even here the distinction is not absolute, for one case is known in which the hybridization of subspecies produced a more atypical pattern than did crosses with four other species (Table VI, compare 93, 95 with 82, 84-88; 113-116 with 96-98).

In his illuminating discussion of homology, de Beer (1958) cited a case of pigment pattern modification in a moth that closely resembles the situation in two geographically isolated populations of *Xiphophorus maculatus* described by Gordon (1951a). When a platyfish from the Rio Coatzacoalcos that carries the *spotted dorsal* gene (Sd) is crossed with a platyfish from the Rio Jamapa, the expressivity of the gene is enhanced, the pattern in the hybrid covering a considerably greater area of dorsal fin and adjacent body than the *spotted dorsal* of either pure race, both of which are very similar in appearance. Similarly, when Ford (1953) crossed individuals belonging to a dark subspecies of *Triphaena comes* from two widely separated islands, the expression of the pattern was modified. Since other tests had shown that the same principal gene was responsible for the color pattern on both islands, the change in its expressivity in the hybrid must have resulted from the interaction of two different systems of genetic modifiers, each of which had nevertheless been responsible for producing an identical phenotype. De Beer (1958) concluded that although the two pigment patterns were pheno-

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[12] A difficulty of this hypothesis is that it makes no provision for the development of the multiple allelism often associated with polymorphism. It therefore implies that despite the apparent similarity of the polymorphism of *X. maculatus* and *X. variatus* to that found in other kinds of animals (most notably insects), its origin has not been the same (see, for example, Ford, 1957).

typically alike and were controlled by the same principal gene, they were not homologous since they were the result of parallel evolution from a common ancestor that undoubtedly did not exhibit the dark pattern, at least not in the form in which it exists at present. The same conclusions could be reached with regard to the situation Gordon found in *X. maculatus.*

A somewhat different situation has been found in two of the subspecies of *X. variatus.* Each of these has at least one *spotted* (Sp) macromelanophore pattern, and the two studied at this time are morphologically distinguishable (see p. 162). In only one of a number of crosses between *X. v. variatus* and *X. v. xiphidium* did any sign of atypical expression of their spotted patterns occur (Table VI, compare 77 with 61-65, 75, 76). Evidently these two alleles are similar enough to be controlled by the same set or sets of modifying factors, and evidently the constellation of modifying genes is the same or nearly the same in both subspecies. Nevertheless, when associated with hybrid genomes involving two other species, *X. p. pygmaeus* and *X. montezumae cortezi,* these alleles react quite differently (Table VI, compare 58-60 with 72, 73; 57 with 69-71). Presumably the relatively slight difference between them could become manifest in a genetic environment where the major gene and approximately half of its polygenic modifiers were not mutually adapted and therefore allowed less "margin for error" during ontogenesis, that is, maintained a lower level of genetic homeostasis.

c. Atypical Pigmentation Associated with the Sc Gene.

Kosswig (1936) was the first to describe the enhancement of the *spotted caudal* pattern (Sc) of *X. montezumae cortezi* in hybrids with *X. hellerii.* In a preliminary report, Gordon (1947b) pointed out that melanomas were obtained "not in the first generation hybrids, but in some of the backcrosses of the hybrids to *X. hellerii* and in some of the second inbred generation." According to the Laboratory data gathered together in Table VI, melanotic overgrowths were obtained among the second backcross hybrids and in the second inbred generation of the first backcross hybrids (nos. 103 and 109). The specimens available at the present time show the following general relationships between type of cross and severity of pigmentary abnormality:

F_1—enhancement

1st backcross—melanosis
    Inbreeding, 1st generation—enhancement
    Inbreeding, 2nd generation—melanoma

    Inbreeding, 3rd generation—melanoma
    Inbreeding, 4th generation—melanosis
2nd backcross—melanoma
    Inbreeding—melanoma
3rd backcross—melanoma
    Inbreeding—melanoma

The percentage of melanomatous individuals in any one brood varied from, roughly, 5% to 30%. The variability of the extent to which melanoses and melanomas were exhibited by various backcross broods may indicate that the factors favoring enhancement of pigment cell growth are not uniformly distributed in *X. hellerii.* There is, however, a complicating factor that makes the results appear distinctly less uniform than those from comparable crosses between *X. hellerii* and macromelanophore-carrying *X. maculatus,* namely, the slow development of melanosis and the late appearance of melanoma among these fish. For example, in our present strain of melanomatous *hellerii-cortezi* hybrids (RJ), which is maintained by repeated backcrossing to *X. hellerii,* overgrowths do not appear until the fish are nearly two years old (Klaus D. Kallman, personal communication). Unless all specimens are maintained for uniformly long periods of time, which was not the case with those discussed above, an uncontrolled variable of major proportions will have been introduced.

Gordon & Nigrelli (1949) briefly described the histology of the overgrowths associated with the Sc pattern. They found that these melanomas somewhat resemble the others that occur in the tail region of various hybrids—presumably associated with Sp, Sb and Sd of *X. maculatus* since these factors also lead to overgrowths on the caudal peduncle. As in all of the melanomas, melanosis always precedes the appearance of any Sc overgrowth. This sequence has been witnessed several times, and individuals with overgrowths always had well developed melanoses while the reverse was frequently not the case. The extensive invasion of tissues by black pigmentation begins near the juncture of caudal fin and peduncle, that is, the general location of the Sc pattern. The gradual encroachment of the melanosis up the caudal peduncle and, subsequently, the body has been observed, but all excessive pigmentation does not arise from this single spreading concentration. In many of the Sc hybrids, clusters of macromelanophores were seen in areas quite far anterior to the melanotic region on the peduncle (Figs. 16, 17). Slashes of intensely black pigmentation also sometimes appeared in the dorsal fin and, less frequently, the pectorals. The latter, it should be

noted, are never pigmented in normal fish of either of the parental species. Whether these islands of macromelanophores hasten the forward advance of melanosis or contribute materially to its development cannot be determined from preserved material, but it seems likely. In general, the number of clusters of macromelanophores could be roughly correlated with the extent of pigmentation of the hybrid brood in question, but this was not always the case. For example, clusters of macromelanophores were seen in seven fish that showed no sign of the Sc pattern (4 from no. 107, 1 from 109 and 2 from 112). The smallest specimen that exhibited macromelanophore clusters was 9 mm. in standard length.

The cases of extreme melanosis, involving at least half of the body in addition to the tail, and those of melanotic overgrowths, were not distributed equally between the sexes of Sc hybrids:

No. males with extreme melanosis 6
No. males with melanoma 0
No. females with extreme
  melanosis as well as melanoma 3
No. females with extreme
  melanosis but without melanoma 1
No. females with melanoma but
  without extreme melanosis 11

The melanoses of the males tended to be greater, even when compared with the most extremely melanotic females. One second backcross male (h42) was completely melanotic except for the eyes and tip of the gonopodium. No connection between sex and melanosis or melanoma has ever been established in the hybrids of *X. hellerii-X. maculatus*, and Berg & Gordon (1953) found melanomas in five hybrids that had no detectable gonads. Nevertheless, the possibility that sex hormones or some genetic factor associated with sex may influence melanoma development in hybrids among the species of *Xiphophorus* may again be broached, on the basis of present observations.

Gordon (1956a) presented a brief, popular account of the origin of the Red Jet (RJ) strain in which he called attention to two noteworthy genetic interactions responsible for the striking red and black coloration of these fish. The strain originated with the crossing of a *wagtail* swordtail with an Sc-bearing member of the inbred offspring of a second backcross to *X. hellerii* of *hellerii-cortezi* hybrids (Table VI, no. 112). The *wagtail* fish must have acquired its pattern through hybridization with *X. maculatus* carrying the *comet* (Co) factor (Gordon, 1946), and therefore a modicum of genes from that species must be present in the Red Jet

strain. Gordon (1956a) reported that in this strain, the macromelanophore *spotted caudal* (Sc) pattern is more enhanced when the micromelanophore *wagtail* (CoE) pattern is present.

This factor interaction is similar to the one between the micromelanophore *stippled* (St) and macromelanophore *spotted* (Sp) patterns in *X. maculatus* which Gordon (1928) also described. That this interaction takes place between cells or elements of tissue is indicated by the very localized enhancement of macromelanophore patterns that is occasionally seen at places on the bodies of hybrids where concentrations of micromelanophores occur. For example, an F_2 fish from the cross of a *striped, one-spot* (SrO) *X. maculatus* with *X. couchianus* (Table VI, no. 36) exhibited a large, melanotic spot on either side of the caudal peduncle, where the *one-spot* pattern is located. The Sr pattern in this fish was barely perceptible, that is, it showed reduced expressivity. At least one other sib, and perhaps three, showed an early stage of a similar macromelanophore spot. In the latter three fish, the Sr pattern was fairly well developed but not enhanced in any way— except in the immediate vicinity of the *one-spot*.[13]

Gordon (1956a) indicated that the red coloration of the Red Jet strain was the result of an enhancement of the three or four horizontal red stripes characteristic of the subspecies *X. hellerii guentheri*. Gordon (1948, 1950a) had described how the red-colored patterns of *X. maculatus* are enhanced in *hellerii-maculatus* hybrids and how erythrophoromas appear, in rare instances, among such hybrids. Similar interactions can occur in other kinds of hybrids, and we have seen *X. maculatus-X. couchianus* hybrids in which the *red dorsal* (Dr) pattern of the common platyfish parent was considerably enhanced. Kosswig (1937, 1948, 1959) has indicated that the same pattern is enhanced in hybrids with *X. v. variatus* and that similar intensification and spread of red pigment patterns occur in hybrids with *X. variatus xiphidium*.

3. Further Aspects of Hybridization.

In his critical review of what is known about hybridization among North American fishes, Hubbs (1955) states that "It has proved to be an almost universally valid rule that natural inter-

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[13] Another indication of localized interaction between pigment cells is the halo effect in which a macromelanophore spot is surrounded by an area that appears to be free of all melanophores. (See Fig. 13.) Enzymatic competition for a limited amount of substrate might be the explanation, and a search for unpigmented pigment cells within the halo should be made. (See p. 162 for additional comment on the halo effect.)

specific hybrids are intermediate between their parental species in all characters in which those species differ, whether they be external or internal, of shape, color, form, structure, or numbers of parts (vertebrae, gillrakers, finrays, teeth)—except for some features that reflect hybrid vigor." There is no question that the overall appearance of the vast majority of fish hybrids is intermediate between the parental forms, but when a detailed, character-by-character comparison is made, an appreciable number of characters may be found to resemble one parent only. The present hybrids illustrate this very well (Table II), and numerous other examples have been reported in the literature (Atz, 1959a). Such instances of "dominance" do not, of course, indicate that the character in question is inherited in a simple Mendelian fashion, as Newman (1914) recognized. The genotypes of even closely related species differ in many genes (Dobzhansky, 1937), and polygenic inheritance is to be expected in the vast majority of cases. There may exist, however, some regular association between the relative amounts of "dominance" and intermediateness that are exhibited by an F_1 hybrid and the phylogenetic relationship of the parental forms. The more closely related the parents are, the less loci are involved in genetic differences, not only in the aggregate but presumably in the control of individual characters as well. The smaller the number of different alleles involved in determining a character, the greater the chance of those from one parent being completely dominant over those from the other. From this it may be deduced that, in general, the greater the proportion of F_1 hybrid characters resembling one of the parental forms rather than being intermediate, the closer to each other are the parents phylogenetically. This may be the reason why a relatively large proportion of characters in the present hybrids show "dominance" of one parental character or the other, while many of the hybrids described by Hubbs and others are intermediate to a significantly greater extent. Moreover, there are instances among the present hybrids in which a character unlike that in either parental form appeared, or in which a character resembling that found in a third species appeared (see item 11 on p. 158).

Results remarkably similar to the ones obtained with the present hybrids were described by Newman (1914) for the pigmentation of F_1 hybrids among *Fundulus heteroclitus, F. majalis* and *F. diaphanus*.[14]

Although the present specimens were not examined for signs of hybrid incompatibility other than pigmentary ones, this phenomenon was manifest in abnormal sex ratios and the presence of large, sexually undifferentiated fish. In general there was a shortage of males, which is in accord with Haldane's Rule that the heterogametic sex is more likely to be sterile, rare or absent in animal hybrids. As far as is known, the male *Xiphophorus* is heterogametic save for the platyfish that inhabit British Honduras (Gordon, 1957). These and other manifestations of hybrid incompatibility have been discussed in detail by Rosen (1960). We need only point out that in no species combination where a concerted effort has been made has it proved impossible to obtain F_1, F_2, F_3 or backcross generations.[15] Hybrid sterility may in fact exist between some species of *Xiphophorus*, since reduced fertility is frequently encountered, but this has not yet been demonstrated.

It must be clear from the preceding discussion (see especially pp. 172-173) that atypical pigment cell growth in *Xiphophorus* cannot be considered an isolating mechanism, as Crew (1940) and Stebbins (1958) have done. That some isolating mechanism must exist is evident, however, from the following observations: (1) *X. hellerii* and *X. maculatus* are found side-by-side in several river systems in southern Mexico, Guatemala and British Honduras; *X. hellerii* and *X. v. variatus* both inhabit at least one tributary of the Rio Nautla; *X. v. variatus, X. p. pygmaeus* and *X. montezumae cortezi* exist close to one another in the Rio Axtla and all three species have been caught there in a single pool (by Gordon, Atz and F. G. Wood, Jr. in 1948); (2) All of these particular species combinations have produced hybrids in the laboratory (Table I);(3) Among thousands of specimens of *Xiphophorus* collected in nature, not a single hybrid has ever been discovered (Rosen, 1960). Laboratory studies (Clark, Aronson & Gordon, 1954) and data collected in the field (Rosen, 1960) indicate strongly that a complex of factors, is responsible for keeping the sympatric species of *Xiphophorus* reproductively apart. The relative importance of the several factors and details of how they operate have yet to be determined.

V. Summary

1. Previous genetic studies of fishes of the genus *Xiphophorus* have concentrated on *X. maculatus, X. hellerii* and their hybrids. The

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[14] This paper was not seen until after the present data had been gathered and analyzed.

[15] Tri-hybrids have been produced involving *X. maculatus, X. variatus* and *X. couchianus* (Table VI, nos. 21, 32, 68, 81) and *X. maculatus, X variatus* and *X. hellerii* (Kosswig, 1935a,b). The former were never bred, but Kosswig found that the latter were fertile.

present studies are principally concerned with five additional species and subspecies (*X. couchianus, X. variatus xiphidium, X. v. variatus, X. montezumae cortezi, X. pygmaeus pygmaeus*) and may be summarized by stating that they confirm and extend the work of Myron Gordon on this group of poeciliid fishes.

2. The pigmentary patterns of these fishes may be separated into monomorphic and polymorphic components and the latter into patterns composed of micromelanophores or macromelophores. The behavior of the monomorphic patterns in hybrid crosses shows that they are controlled by polygenes and that, in some cases the number of genes involved is not large.

3. The changed appearance of polymorphic pigmentary patterns in various hybrid combinations also reveals probable methods of genetic control; both micro- and macromelanophore patterns are undoubtedly influenced by constellations of modifying genes. A few new examples of modified tail patterns (micromelanophore) and several of spotted patterns (macromelanophore), including the *spotted caudal* pattern, have been studied. In hybrids, tail patterns resembling the *wagtail* and *Guatemala crescent* and spotted patterns ranging from zero penetrance to melanosis and melanoma production have been observed.

4. The major pigment cell genes vary in their ability to produce melanosis and melanoma in hybrids, and the species vary in their ability to control the growth of pigmentary patterns from other forms. *X. maculatus*, which possesses the genes most potent in producing atypical pigment cell growth in hybrids, is also the only species in whose hybrids no enhancement of macromelanophore patterns from other species ever occurs.

5. This indicates a similarity of biochemical processes among all the major genes for macromelanophore patterns, but a highly developed specificity also exists, because in the same hybrid individual, the expressivity of one macromelanophore pattern may be increased while that of another is reduced or remains unchanged.

6. The concept of genetic homostasis, as developed by Schmalhausen and by Lerner, has proved useful in explaining departures from the results expected in typical polygenic inheritance and also the differences in expressivity in hybrids of genetic factors that act practically the same when associated with genomes more like their normal ones.

7. The appearance, in various hybrids, of the *spotted* patterns of *X. variatus xiphidium* and *X. v. variatus,* and crosses between *X. montezumae cortezi* and *X. m. montezumae,* indicate that the same kinds of genetic differentiation occur in subspecies as in species.

8. The frequency with which the characters of hybrids resemble those of either parent, rather than being intermediate, may be a measure of the phylogenetic relationship of the parental forms. The more closely these are related, the greater the proportion of characters that are not intermediate.

9. No absolute hybrid sterility between any of the fishes of the genus *Xiphophorus* has ever been demonstrated. Although the abnormal expressivity of pigment genes in hybrids leads to lethal melanoma in some crosses, it seems never to have served as an isolating mechanism.

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EXPLANATION OF THE PLATES

Living and preserved fishes photographed by Sam Dunton, Photographer, New York Zoological Society. Prepared skins photographed by Dr. Ross F. Nigrelli, Pathologist, New York Aquarium, New York Zoological Society.

Dimension of fishes is Standard Length and is approximate.

PLATE I

Fig. 1. Hybrid *X. maculatus* × *X. variatus xiphidium*. Male on the right shows *wagtail*-like modification of *comet* (Co) pattern of *maculatus* and slightly suppressed *spotted* pattern of *variatus*. Both males show the *crescent* (C) tail pattern. See Table V and Table VI, nos. 26, 79.

Fig. 2. Backcross offspring, males (*X. maculatus* × *X. v. xiphidium*) × *X. v. xiphidium* Upper fish exhibits *wagtail*-like modification of *comet* (Co) pattern. See Table V and VI, no. 80.

Fig. 3. Hybrid *X. v. xiphidium* × *X. maculatus*. Female (32 mm.) on right, exhibits a slightly enhanced *striped* (Sr) pattern from *maculatus*. Male (30 mm.), on left, exhibits *spotted* (Sp) pattern from *xiphidium*. See Table VI, nos. 27, 37, 78.

PLATE II

Fig. 4. *Xiphophorus v. variatus,* female (40 mm.), on left. Hybrid, *X. maculatus* × *X. v. variatus,* male (35 mm.), on right. Male exhibits *spotted* (Sp) pattern from *variatus,* the spots being small and located in front of and under the dorsal fin. Male also exhibits *spotted* (Sp) pattern from *maculatus,* the spots being large and located under the dorsal fin and behind it. (P_1 of h61).

Fig. 5. Backcross offspring, females (31-35 mm.), showing different degrees of enhancement of the *spotted* pattern from *maculatus.* (h61).

Fig. 6. Backcross offspring, males. Two upper fish exhibit the *spotted* pattern from *variatus*; lowest, exceptional fish the *spotted* pattern from *maculatus.* Three exceptional (crossover?) males and one female appeared among 41 females and 53 males. No fish exhibited both *spotted* patterns, thus, indicating that the two Sp factors are alleles. (h61). See Table VI, nos. 17, 56.

PLATE III

Fig. 7. Hybrid *X. v. xiphidium* × *X. v. variatus.* Both fish exhibit an enhanced *spotted* (Sp) pattern from *xiphidium.* Female, on right, also exhibits the *spotted* (Sp) pattern from *variatus,* the spots of which are much smaller and lighter. Male, on left, exhibits a modified *cut-crescent* tail pattern; female (35 mm.) a typical *upper cut-crescent* pattern. See Table V, Table VI, nos. 65, 77.

Fig. 8. Hybrid *X. couchianus* × *X. v. variatus.* Female, above, exhibits *spotted* (Sp) pattern from *variatus.* See Table VI, no. 53.

PLATE IV

Fig. 9. Hybrid *X. montezumae cortezi* × *X. v. variatus.* Female, on right, exhibits *spotted* (Sp) pattern from *variatus.* See Table VI, nos. 57, 97.

Fig. 10. *X. m. cortezi* × *X. v. xiphidium.* P_1 male (25 mm.), upper right, exhibits the *spotted* (Sp) pattern. P_1 female (35 mm.), upper left, exhibits no macromelanophore pattern. F_1, lower left, exhibits strongly enhanced *spotted* pattern from *xiphidium*; F_1 lower right, exhibits no macromelanophore pattern. See Table VI, no. 69.

PLATE V

Fig. 11. Hybrid *X. v. variatus* × *X. p. pygmaeus.* Male (25 mm.), below, exhibits *spotted* (Sp) pattern from *variatus.* As this fish grew older, the spots increased several times in size and new ones appeared in abnormal locations. See Table VI, no. 58.

Fig. 12. Hybrid *X. p. pygmaeus* × *X. v. xiphidium.* Female, on left above, exhibits strongly enhanced *spotted* (Sp) pattern from *xiphidium.* See Table VI, no. 72.

PLATE VI

Fig. 13. *X. m. cortezi* × *X. hellerii strigatus.* P_1 female, on left below, exhibits *spotted* (Sp) pattern. F_1 male, on right above, exhibits same *cortezi* pattern but with reduced expressivity. See Table VI, no. 88. Note prominent reticulum of *cortezi.* (h9).

Fig. 14. Backcross offspring of h9 to female *X. h. strigatus.* Female (40 mm.), on right above, exhibits *spotted* (Sp) pattern from *cortezi* with reduced expressivity. See Table VI, no. 89.

PLATE VII

Fig. 15. *X. m. cortezi* × *X. h. strigatus.* P₁ female, on right, middle, exhibits *spotted caudal* (Sc) pattern, which F₁ female (40 mm.), above, exhibits in an enhanced form. P₁ male, on left, below. See Table VI, no. 99. (h26).

Fig. 16. Second backcross offspring of h26 to male *X. h. strigatus.* Female (50 mm.) exhibits melanotic caudal fin and peduncle with an overgrowth. Note slashes of pigment in dorsal fin and several melanophore clusters on body, at least one of which is located anterior to the dorsal fin. See Table VI, no. 103.

Fig. 17. Cleared skin from side of *cortezi-hellerii* Sc hybrid (353) showing macromelanophore cluster and faint mid-lateral stripe. Anterior to the right. About 15½ ×.

Fig. 18. Cleared skin from side of wild male *X. v. variatus* showing reticulum, *spotted* pattern and vertical bar (at center). Anterior to the right. About 14¾ ×.

PLATE VIII

Fig. 19. *X. h. guentheri* from the Belize River in British Honduras, female above, male below. Both fish exhibit the *spotted* (Sp) pattern.

Fig. 20. Hybrid *X. h. guentheri* × *X. maculatus.* Fish on the right exhibits *spotted* (Sp) pattern from *guentheri.* Fish (50 mm.), on the left, exhibits a peculiar, undiagnosed atypical growth not associated with Sp. See Table VI, no. 119. (320).

Fig. 21. Backcross offspring of 320 to male *X. maculatus.* Male exhibits *spotted* (Sp) pattern from *guentheri* and nearly completely suppressed *striped* (Sr) pattern from *maculatus.* See Table VI, nos. 40, 127.

Fig. 22. Inbred, second backcross offspring of 320 to female *X. maculatus.* Female (28 mm.), exhibits *spotted* (Sp) pattern from *guentheri* and *striped* (Sr) pattern from *maculatus.* See Table VI, nos. 52, 126.

PLATE I
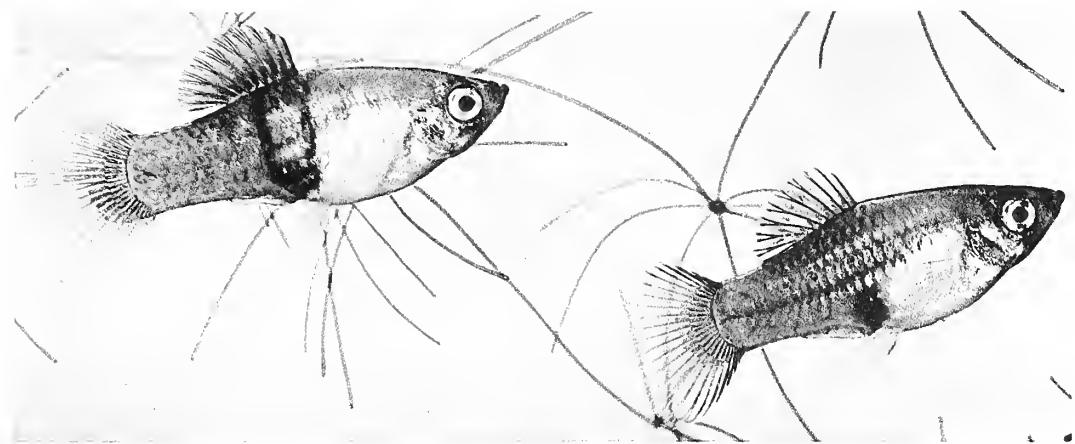
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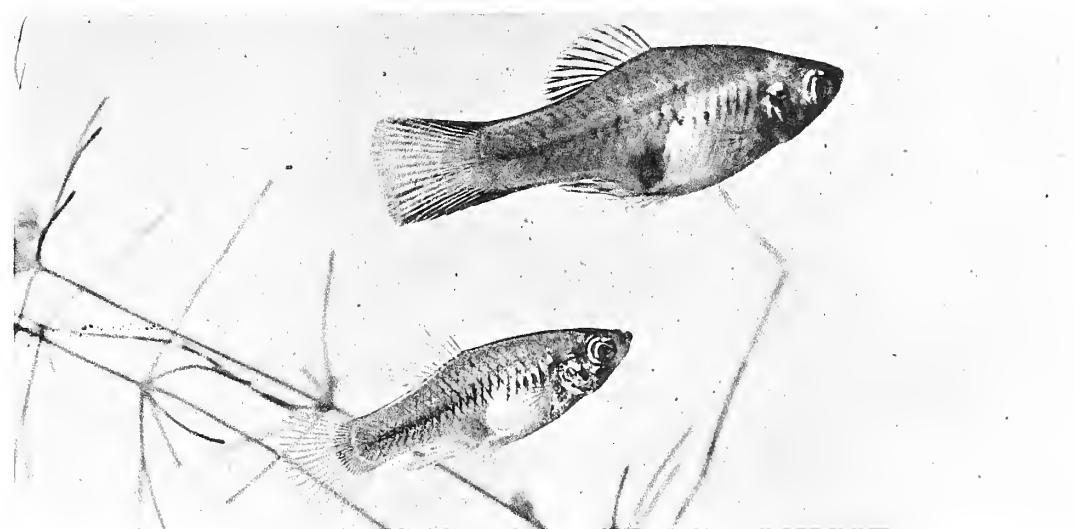
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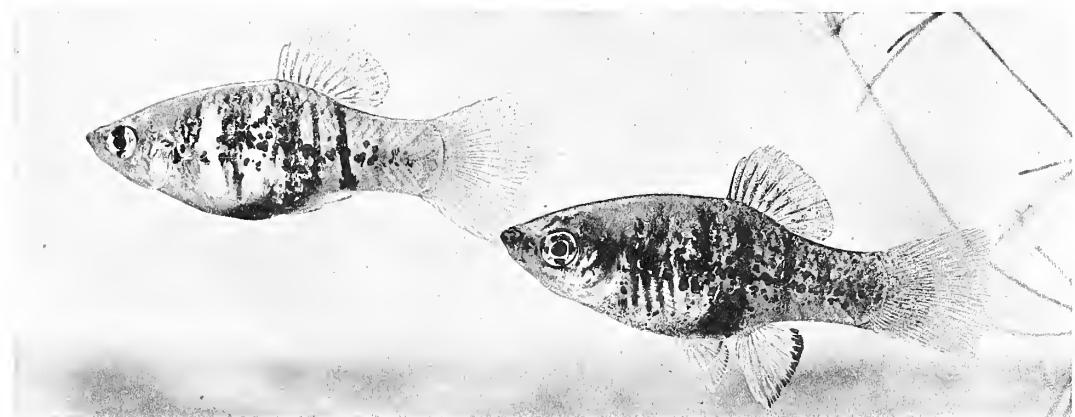
FIG. 3

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS

PLATE II
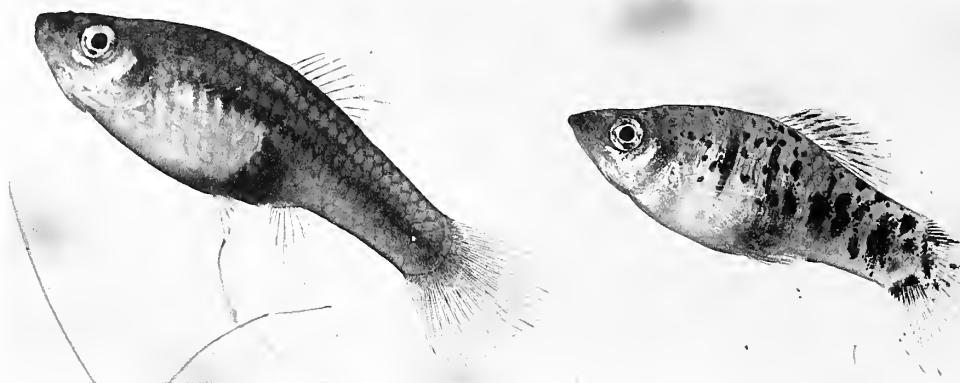
FIG. 4
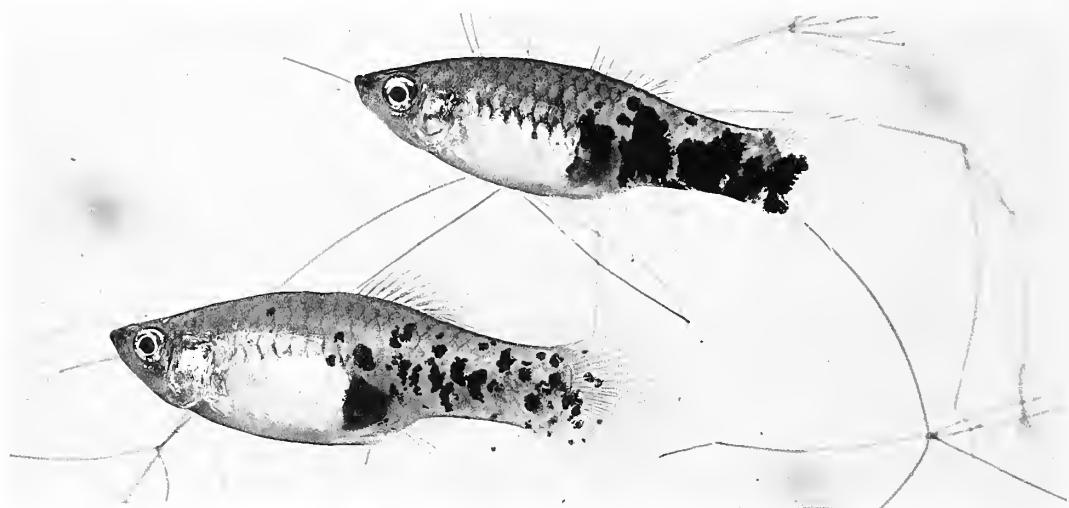
FIG. 5
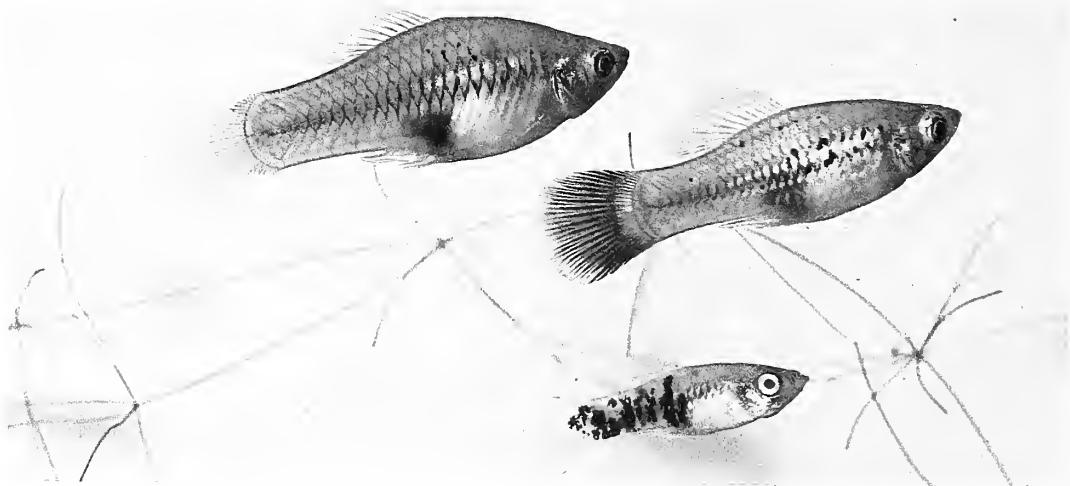
FIG. 6

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS
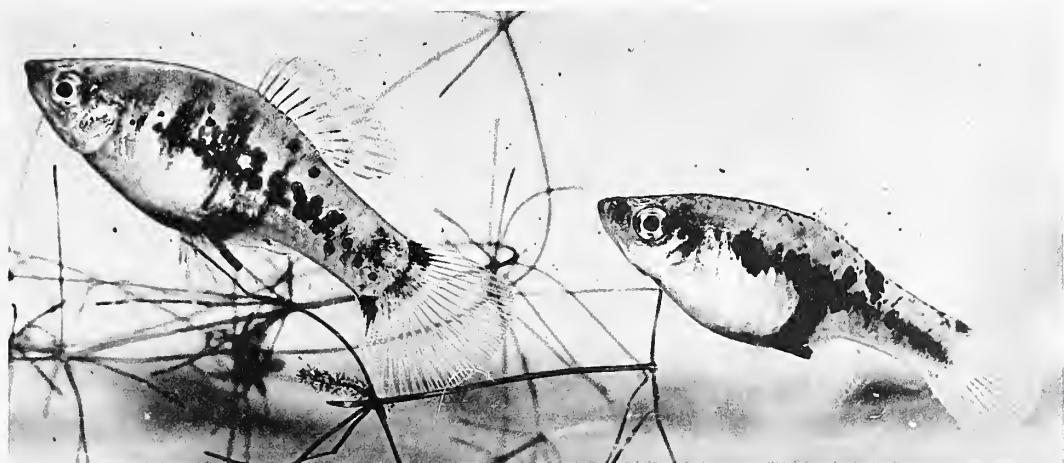
FIG. 7

FIG. 8

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS
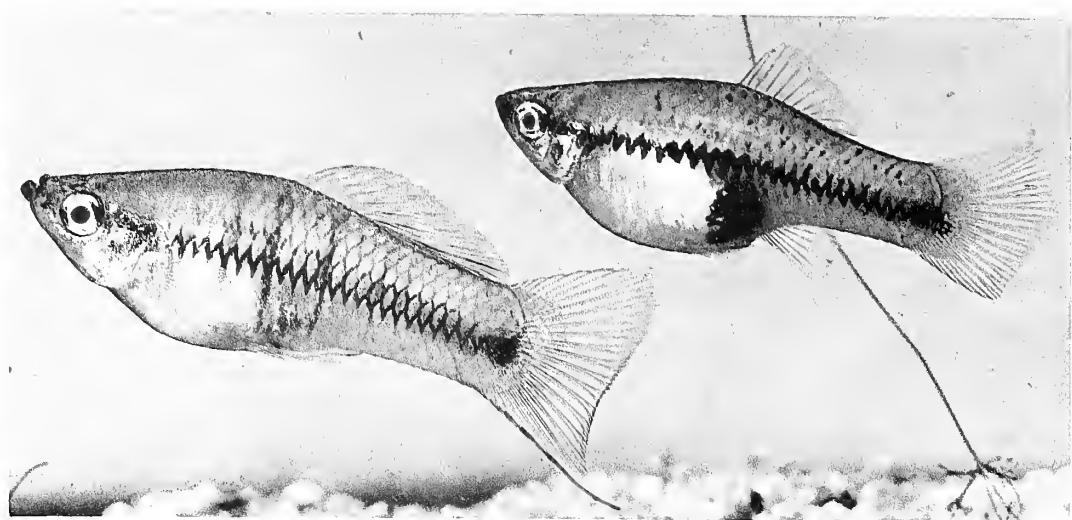
FIG. 9

FIG. 10

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS
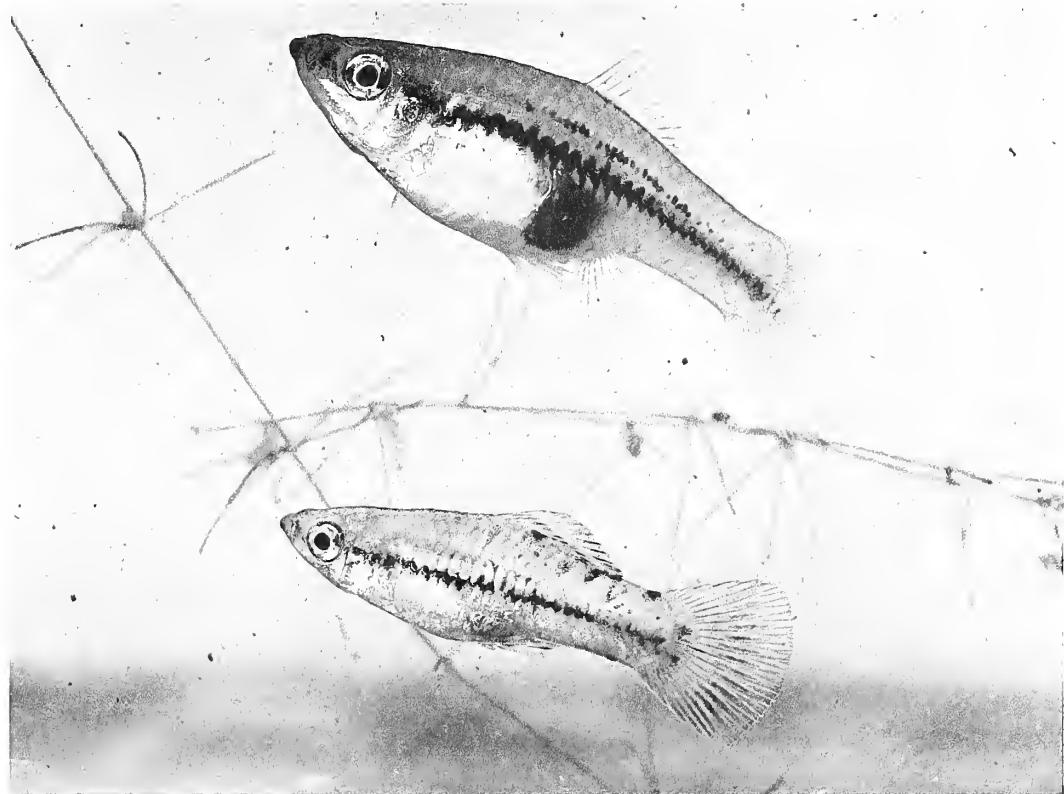
FIG. 11

FIG. 12

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS
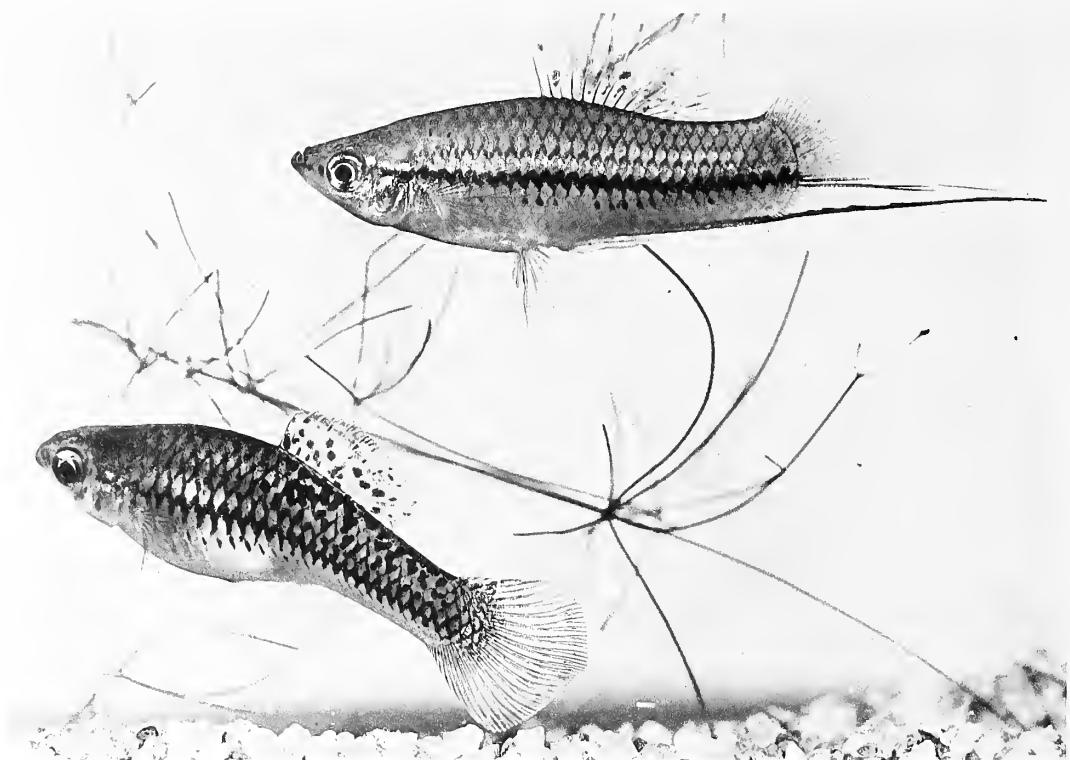
FIG. 13
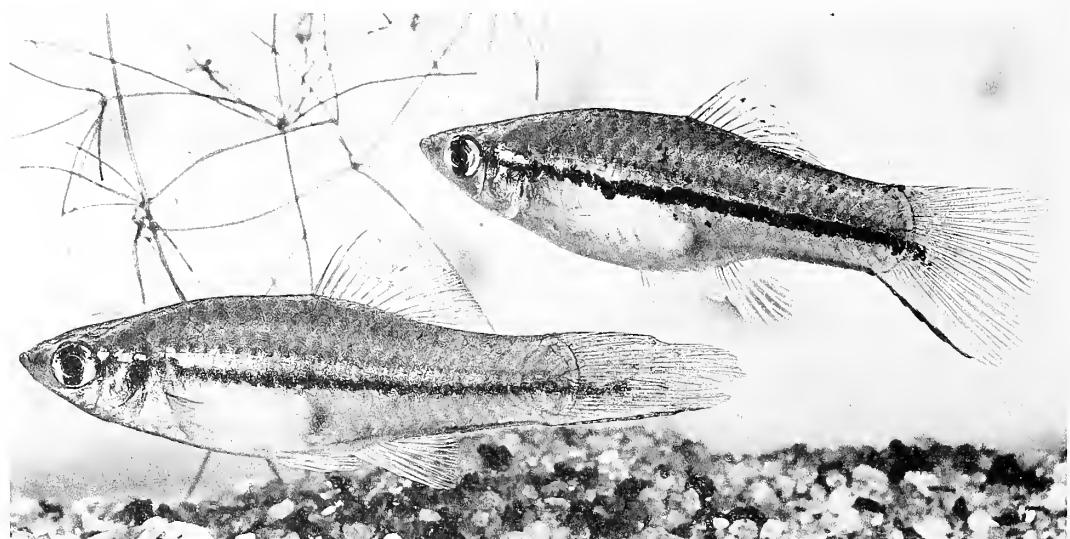
FIG. 14

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS

FIG. 15

FIG. 16
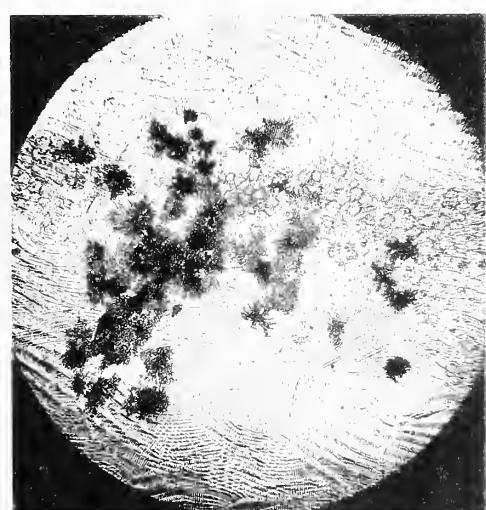
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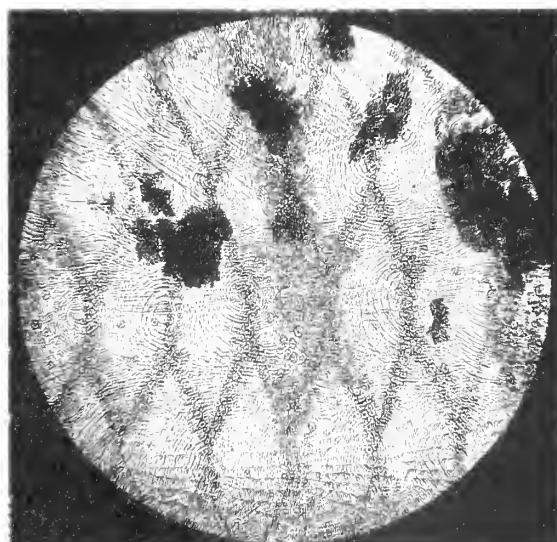
FIG. 18

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS
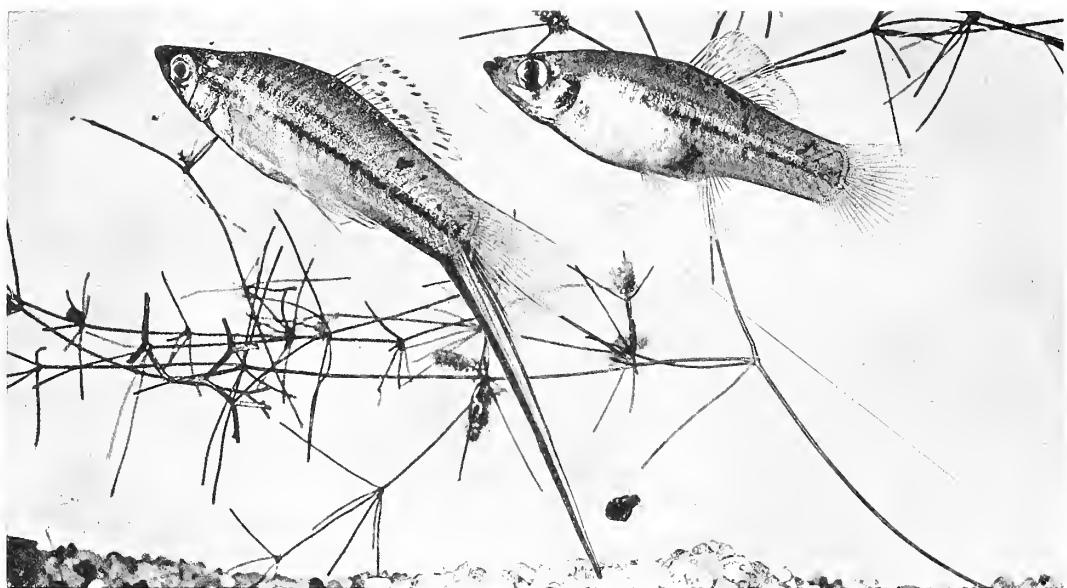
FIG. 19
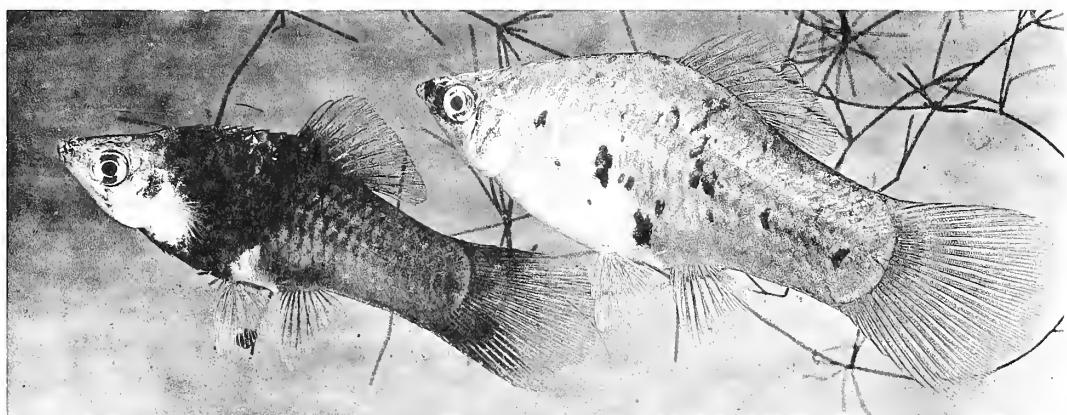
FIG. 20
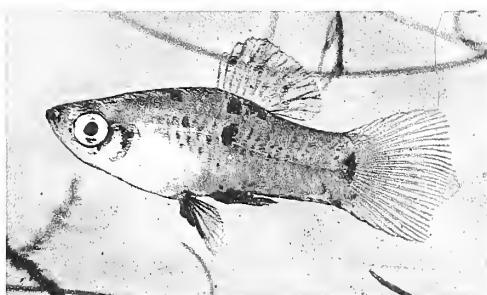
FIG. 21
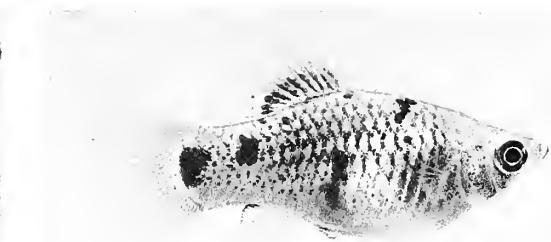
FIG. 22

EFFECTS OF HYBRIDIZATION ON PIGMENTATION IN FISHES
OF THE GENUS XIPHOPHORUS

15

A Field Study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad, W. I.[1,2]

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(Text-figures 1-6)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest preserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe, Zoologica, 1952, 37 (13): 157-184.]

INTRODUCTION

THIS paper is to some extent complementary to a previous paper on the Black and White Manakin, *Manacus manacus* (Snow, 1962). Both species were studied at the same time, largely by the same methods, and in the same locality, an area of primary and secondary forest in the center of the Northern Range of Trinidad.

About 3½ inches long, the Golden-headed is a smaller and lighter bird than the Black and White Manakin. Its bodily proportions are different; its wings are relatively and absolutely longer, and its legs and tail shorter. Correspondingly, its flight is more rapid and agile, and its displays depend more on flight and wing actions and less on jumping. The male is all black, with a golden-orange cap and red and white thigh feathers; the female is olive-green. The eye is white in the male and the beak pale brown or straw-colored; in the female the eye is variable in color, but darker, and the beak is darker brown. Like other manakins, Golden-headed Manakins feed largely on fruit, which they take on the wing, but insects are also taken. They bathe in streams, and drink from water collected in the leaves of trees.

For a field study, the Golden-headed is less suitable than the Black and White Manakin. Although it is the more abundant species, at least in Trinidad, most of its activities are carried out higher above the ground. It feeds on average higher, it displays up in the trees, at a height of 20 feet or more, and its nests are placed on average much higher above the ground. Also, its very abundance made it difficult to band more than a fraction of the local population. Over 600 individuals were banded in the study area, but when trapping ceased new birds were still being caught far more often than previously-banded birds. Thus much less detailed information was obtained for the Golden-headed than for the Black and White Manakin, especially as regards nesting and the histories of individual birds.

For details of the environment, the reader is referred to the earlier paper. Here it need only be said that the vegetation is transitional between seasonal forest and lower montane rain forest (Beard, 1946); the temperature varies little throughout the year; annual variation in daylength is 74 minutes; the rainfall averages about 100 inches per year; there is a main dry season from January to May, and the wet season lasts for the rest of the year, being usually interrupted

by a short spell of dry weather in September or October.

Apart from Skutch's study of *P. mentalis* (Skutch, 1949), no detailed study has been made of any species of *Pipra*. A preliminary account of the present work, dealing only with display, has already been published (Snow, 1956). Sick (1959) has described displays of *P. erythrocephala* and *P. fasciicauda.* Niethammer (1956) has briefly described displays of *P. chloromeros;* and Snow has described displays of *P. pipra* and *P. aureola* (Snow, 1961 and in prep.). (I have referred to "displays" and not "the displays" advisedly, as these studies are certainly not complete; I have always found that manakin species, when watched intensively over a long period, reveal a greater repertory of distinct displays than is apparent from more cursory observation). From these studies it is known that the males of some species of *Pipra* display communally, and some solitarily. Of the known species, *P. erythrocephala* is one of those in which communal display is most highly developed.

Since many comparisons with the Black and White Manakin are made in the course of this paper, for brevity I refer to my previous paper simply as *"Manacus,"* followed by the relevant page-number in that paper.

As in the previous paper, I am indebted to several persons for help with the field work; especially to my wife, for much help in the mist-netting and in finding nests; to Dr. W. G. Downs and Dr. T. H. G. Aitken, for making available to me the birds trapped in the course of the work of the Trinidad Regional Virus Laboratory; and to Mr. N. Y. Sandwith and Dr. J. J. Wurdack for many plant identifications. The whole work was generously supported by National Science Foundation Grants G 4385 and G 21007.

The Population

The Golden-headed Manakin is probably the most abundant forest bird in Trinidad. At the main trapping place, on the edge of secondary forest, and at two subsidiary trapping places two and four hundred yards inside the forest, 625 different individuals were caught over a period of 3¼ years. When trapping ceased, as already mentioned, more new individuals were still being caught than previously-banded birds. In the last four months of trapping, 89 new birds and 32 previously-banded birds were trapped. Up to that time, 529 individuals had been caught. Allowing an annual mortality of 10% (see later in this section), about 440 of these would have been expected to be still alive. With the proportion of recaptures to total captures at 32/121 or 26%,

the total population from which the captured birds were drawn should have been of the order of 1,700.

This calculation is clearly subject to considerable error, as the ringed and unringed birds were certainly not randomly mixed within the population, and it is not known how far individuals range in the course of their daily activities. Probably most of those caught lived within the steep-sided forested valley, of about 200 acres, formed by the stream along which the trapping places were situated. It may reasonably be supposed that the density of Golden-headed Manakins in this area was certainly more than one per acre, and probably several times as great.

The Black and White Manakin, probably the next commonest species of forest bird in the study area, was found to have an adult density of just over one bird per acre.

The annual mortality of adults can be estimated approximately from the proportion of adult males in the population. Of the first 100 birds caught at the main trapping places (feeding and bathing places away from the display grounds), 45 were adult males. Of the second 100 caught, 44 were adult males. Thereafter the proportion of adult males declined to around 35% and remained at this figure. This decline was probably due to the fact that adult males are more sedentary than females and young birds, being closely attached to their display grounds, and many of those whose display grounds were nearest the trapping places had by then been caught and were tending to avoid the trapping area.

Male Golden-headed Manakins moult into adult plumage at the beginning of their second year of life. A population in which the sex ratio is equal (as it is in *Manacus* and probably is also in the Golden-headed Manakin) and 44% or 45% of the individuals are adult males, should have an annual adult mortality of about 10%, a figure that is very close to that obtained for the Black and White Manakin by another method (*Manacus*, p. 96).

The Display Grounds

Male Golden-headed Manakins display communally, but in much more diffuse groups than Black and White Manakins. Each male occupies a particular perch, 20 to 40 feet above the ground. The perch selected is usually a more or less horizontal twig under the canopy of a lower story tree, but sometimes a horizontal stretch of vine is used. To be suitable, a display perch must be roughly straight and without side branches, and not too thick (5-10 mm.). It must have a

clear approach from one side at least, to allow the displaying bird to make the display-flight (p. 186).

The males sometimes peck at excrescences on their display perches, and if there are leaves or tendrils of vine hanging near them they habitually pull at them while hovering or hang onto them. As a result the leaves near a display perch are often tattered. Thus Golden-headed Manakins show in some degree the tendency to clear the display area which is so marked in the Black and White Manakins.

The display perches of different males may be several feet apart in the same tree, or several yards apart in neighboring trees. The number of males at a display ground is variable; those that were studied usually had from six to twelve males.

As in *Manacus* (p. 69), display grounds were found to persist year after year in the same places, and the same display perches were used in successive years. Because it is much less obvious that individual perches are in constant use than it is in *Manacus,* there being no equivalent of the court, the persistent nature of the display ground is not apparent to the observer unless he is able to watch an area over a long period. Probably for this reason, Sick (1959) gives the impression that in Brazil the Golden-headed Manakins display randomly in the forest. In Trinidad, random display could indeed be seen at times all over the forest, mainly from juvenile males, but these birds doubtless eventually settled at one of the permanent display grounds.

Elements of the Display

The Golden-headed Manakin's display movements and postures are highly stereotyped and very diverse. Some are much more often seen than others, and it was not until I had watched the birds for over a year that I saw some of the less common displays. After 5½ years of intermittent observation, with regular weekly watches for the last 13 months of this period, I was confident that I had seen the full range of normal display given by the Trinidad population of the species. As mentioned later (p. 187), there is some evidence that the display differs markedly in the Brazilian population.

As already mentioned, compared with the Black and White Manakin the Golden-headed has relatively long, pointed wings, and short legs. It is extremely agile in flight, and specialized flights are important in its display. It does not hop or jump, but moves sideways or backwards along the perch with very short quick steps that give the bird the appearance of sliding. In resting posture, it sits hunched, with body-feathers fluffed and legs concealed. When it begins to display its appearance changes markedly; it sleeks its plumage and stretches its legs, so that the red and white thigh feathers appear.

In view of the male's extreme agility in flight, it is of interest that he averages a little lighter and smaller than the female (Appendix). In *Manacus,* in which display depends on specialized wing-feathers and hypertrophy of the muscles of the shoulder region and thighs, the males are heavier than the females and their wings are shorter.

In the following sections, I have for convenience used the same names as Skutch (1949) used, for display movements that are clearly homologous with those of *Pipra mentalis.*

Advertising Calls

Males sitting inactive on their display perches frequently utter advertising calls, which can be arranged in a series of increasing excitement leading up to active display. At lowest intensity they utter an occasional clear "pu." When excitement is a little increased this is followed by a trill and usually a sharp final note: "pu prrrr-rrr-pt." With mounting excitement the final note is repeated two or three times, the initial "pu" is replaced by one or two sharper notes, and the trill may be lengthened, so that the call becomes "pir pir prrrrrrrrr-pt-pt." The first note of the call may be accompanied by an upward flick of the wings. At this stage the bird is likely to break into more active display.

The other calls are characteristically associated with particular display movements, and will be described in the following sections.

Darting Back and Forth

With the legs stretched so that the colored thigh feathers show, and the body held rather horizontally, the bird makes rapid flights to and fro between its main perch and an adjacent perch usually 3-5 feet away. When it has landed it at once turns rapidly about to face the way it came from. In flight between the two perches, the wings make a brisk humming sound audible for about 20 yards. Between bouts of darting back and forth, a very short, sharp "zit, zit" is often uttered.

The About-face

Rapid about-faces, such as are made between darts back and forth, may be repeated while the bird remains perched in the same place. Each turn may be accompanied by an upward flick of the wings.

The Backward-slide

With the legs stretched, the head held low and

the tail elevated, the bird "slides" backwards along its perch for several inches (Text-fig. 1, b and d). The line of the body is usually at an angle of about 45° to the line of the perch, but this varies; sometimes the body is held almost in line with the perch, and occasionally nearly at right angles to it. At the end of the slide the tail is suddenly depressed· and fanned, and the wings raised and held vertically above the back (Text-fig. 1, a and e). Half way through the slide, the wings may be suddenly spread horizontally and then closed again (Text-fig. 1, c and f); this movement is often omitted. Very seldom, after sliding one way the bird may turn and slide back in the other direction. This display is silent.

The Display-flight

The male leaves his perch and flies with normal flight to a somewhat higher perch about 20-30 yards away. He perches and faces his display perch, utters usually two or three sharp calls, "kew, kew," then takes off and returns to the display perch with extremely rapid flight, uttering a succession of "kew" calls which speed up and become sharper as he nears it. Usually a total of 7-9 "kew" calls are uttered (including those made before taking off). The bird ap-proaches his display perch with a rapid downward, then upward, then downward swoop, so that its trajectory is a shallow S-curve. As it lands it utters a sharp buzzing call. Thus the listener hears an accelerating series of "kew" calls followed by a sharp buzz, a sequence of sounds that is diagnostic of this display. In this way the display-flights of a group of males can easily be counted even while the observer is watching only one or two of them, as was done during the all-day watch at a display ground described later (p. 190).

Immediately on landing, the bird usually executes a backward-slide. At lesser intensities the slide may not be made, and sometimes the bird lands without uttering the buzzing call. These incomplete displays usually occur if for some reason the bird is put off at the last moment, or apparently misjudges its landing on the perch.

The Frenzied Flutter

This term is used to cover some rather variable movements, having in common that the bird jumps, or makes as if to jump, upwards, and utters an excited "zeek" or "zeek-eek," reminiscent of the buzz made on landing from the display-flight but higher pitched. The bird may
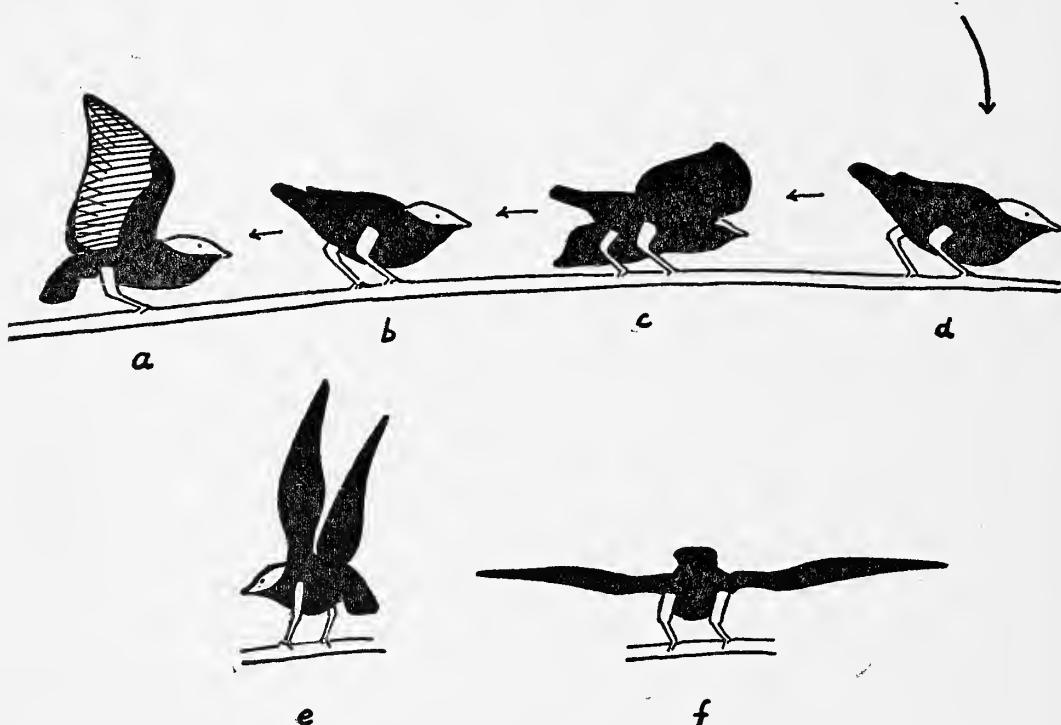
TEXT-FIG. 1. The backward-slide. Arrows show the direction of the bird's movement. b and d: posture while sliding. c and f: wings spread half way through slide. b and e: wings raised and tail fanned at end of slide. a-d shows normal orientation with respect to perch; e and f show less usual orientation transversely to perch. (Drawn from movie film).

jump up or slightly backwards a few inches, with wings conspicuously fluttering, and land back on the same spot; or it may jump up and land a foot or more away with a rapid upward and downward trajectory and a sudden alteration of course in mid-flight; or it may flutter along the perch, moving forwards (not backwards, as when sliding); or it may jump up and flutter, rapidly twizzling from side to side before it lands; or it may simply crouch and flutter its wings violently without leaving the perch. While fluttering it tends to make downward pecking movements which appear to be directed at the perch.

It will be apparent from the foregoing description that this display has much in common with copulation. It is given at times of great excitement and may be thought of as copulation *in vacuo.*

The Upright Posture

When another bird lands on or near a male's display perch, the owner often flies and lands close beside it in a stiff, almost statuesque upright posture (Text-fig. 2). He may not fly straight to the intruding bird, but may make a short circling flight of a few yards away and back, a flight which is sufficiently stereotyped to be regarded as a preliminary part of this display. Just after landing he utters a very sharp, short "zick." The upright posture may be held for several seconds, the bird clinging to the side of the perch rather than perching on it, with the head pointing upwards and the beak often slightly opened. At close quarters it is possible to see that the pupil is greatly contracted while this posture is held. In this display the aggressive element is probably more dominant than in the displays described above. It is often the initial response to an intruder of either sex, and in several cases when it was seen to be made to birds in female plumage there was reason to think that they were young males.

Wing-flicking

General excitement may be shown by quick upward flicks of the wings. Wing-flicks may be interpolated between pivoting, frenzied flutters, and other display movements, or they may sometimes be repeated rapidly by a perched bird and accompanied by the call "pir pir prrrrrrr-pt" or the more excited "zeek-eek." Repeated wing-flicking, with calling, appears to constitute an independent display, but one that is less ritualized than those described above.

Sick's Observations in Brazil

Sick's account of the displays of *Pipra erythrocephala* in Brazil (Sick, 1959: 275-277) differs in several respects from that given here. The Brazilian form (subspecies *rubrocapilla*) is very distinct from the Trinidad form, which is close to the nominate subspecies: the head is red, not golden-yellow, and there is a conspicuous white patch on the under wing-coverts, which is lacking in the Trinidad bird. For the Brazilian bird, Sick does not mention "darting back and forth," the "frenzied flutter" or the "upright posture"; nor does he describe the full "backward-slide" following the "display-flight", which is perhaps the most conspicuous of all the display sequences of the Trinidad birds. He mentions the backward-slide briefly, as being accompanied by quivering of the slightly raised wings, but not the spreading of the wings half way through the slide nor the raising of the wings and fanning of the tail at the end of the slide. He describes the display-flight as silent, whereas in Trinidad, although the flight is unaccompanied by mechanical sounds, the characteristic calls associated with it make it far from silent. He says that wing-flicking on the perch is sometimes accompanied by a snapping sound, which I never heard. Finally, he describes how the white patch on the under-side of the wing is exhibited in display, by a posture to which there is no parallel in the Trinidad bird.
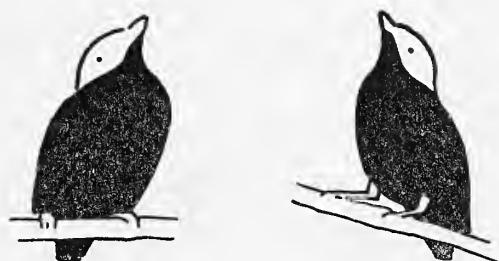
TEXT-FIG. 2. The upright posture. (Drawn from movie film).

Further observations may show that not all these differences are real ones; even so, it seems clear that we have in this species an outstanding example of subspecific differences in display which would repay detailed study. It would be desirable to have a motion picture record of the displays of the Brazilian birds for comparison with the Trinidad population.

RELATIONSHIPS BETWEEN MALES

As in *Manacus* (p. 79), neighboring males usually show little overt aggressiveness towards each other, but they are in fact potentially aggressive. Hostility increases when a female visits the display ground, and it was on such occasions that the few flight chases between adult males were seen. Each male defends its perch against

intruders mainly by means of displays (especially landing beside the intruder in the upright posture, backward-slides, and wing-raising), but fights were never observed, as they were several times in *Manacus,* nor was there any evidence of one male trying to usurp another's display perch. Presumably Golden-headed Manakins can find new display perches more easily than Black and White Manakins can clear new courts, so that serious competition for display perches will be rare.

Neighboring males spend much time sitting quietly side by side on some perch usually between their two display perches. The most striking feature of this behavior is that both birds constantly face away from each other. Sometimes one bird shows its aggressiveness by an occasional backward-slide towards the other, or by suddenly raising its wings and fanning its tail (as at the end of the full backward-slide), and in such cases it may be seen that of the two birds the subordinate one has its head more completely averted than the displaying bird.

As in *Manacus* (p. 80), which has similar behavior, birds sitting with a neighbor spend more time at the display ground than those that are alone. This is especially noticeable when display is slack. Frequently they leave the display ground together and return together, which suggests that they associate together even when feeding. During an all-day watch on April 29, 1961 (p. 190), the male that was being watched continuously (Male A) sat with his nearest neighbor (Male B, whose display perch was only a few feet away in the same tree) for a total of 3 hours 44 minutes, in 48 spells, most of which were from 2 to 6 minutes long. Usually they sat together between their display perches, but sometimes on another perch several yards away in another tree. Male A also several times sat with another male several yards away, and Male B sat with two other males.

More than two males never sit together at the same time. This is a matter of common observation, but it was once seen especially clearly, when Male B was sitting with another male on a perch where he sometimes sat with Male A. Male A was sitting on a lower perch by himself about 30 feet away. The male with B flew off, and Male A, who appeared to have been waiting for this to happen, at once flew up and sat by Male B.

During the moult, when some males are absent, those that remain visit the unoccupied display perches and keep less strictly to their own, exactly as was found in *Manacus* (p. 79). Thus although there seem to be numerous suitable display perches in the area of the display ground, those that are actually "owned" by a male have a special significance for other males. It seems most likely that it is the mere fact that they have been occupied by another male that gives them this significance, rather than that they are especially suitable in some way not apparent to the human observer.

At the display ground that was under regular observation for a year, the display perches of six males were in view from the hide. Of the males that eventually occupied them after the moult, one was unbanded, one was banded with a numbered and a colored ring, and four were banded with numbered rings only and so were not individually distinguishable in the field. (The main trapping area, where over 600 individuals were caught, was about 200 yards away from this display ground.) Except for the unlikely possibility that the similarly banded males changed places with each other without any disturbance in their behavior being noted, these individuals kept to the same display perches throughout the greater part of the period of observation. The only observed changes took place as the time of moult approached; in June the color-banded male moved and displaced one of the banded males from a neighboring display perch, without however completely abandoning his former perch. The displaced male was not seen again, and may in fact have begun to moult (the earliest birds begin in July, Text-fig. 6). In July two more males disappeared and presumably began to moult. The color-banded male began to display occasionally at the perch of one of them, so that he now displayed at three perches. The display perch of the other male that had disappeared (Male A) was occupied by Male B, his close neighbor. The three males that remained were present throughout August, but in early September they all disappeared.

Text-figure 5 shows that a little display was recorded in September at this display ground. It was due entirely to a few newly arrived birds, probably recently moulted young males (p. 194). They did not use the display perches of the old males, but displayed on various perches round the periphery of the display ground.

Behavior of Juvenile Males

On many occasions groups of two or three birds in female plumage were seen away from display grounds performing uncoordinated display in a similar way to that described for juvenile male *Manacus* (p. 80). By analogy with *Manacus* they were assumed to be juvenile males, but this was not proved. Occasionally they were accompanied by adult males. All the
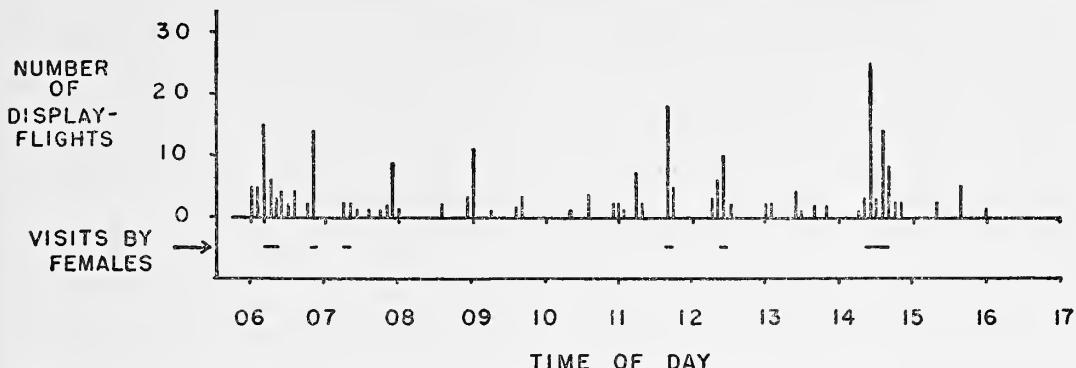
TEXT-FIG. 3. Diurnal rhythm of display, April 29, 1961. Intensity of display measured by number of display-flights in each 5-minute period (vertical lines).

display movements were made, but the display-flight was not usually followed by the backward-slide; displays tended to be incomplete and un-coordinated. In these groups presumed young male Golden-headed Manakins were occasion-ally seen associating with female-plumaged Black and White Manakins, and on one occasion a Black and White Manakin known from its later history to have been a juvenile male was seen displaying quite persistently to a Golden-headed Manakin. Parkes (1961) has discussed these observations in relation to the occurrence of occasional hybrids in the Pipridae.

COURTSHIP AND COPULATION

I was usually unable to be certain of the sex of the female-plumaged birds that I saw visiting the display grounds. The behavior of these birds seemed usually to be more ambivalent than that of the female-plumaged *Manacus* (p. 77), which were normally easy to sex after they had been watched for a little in the field. Eye-color sometimes provided a clue (p. 196), but was not usually observable accurately enough from a distance of several yards. Few color-banded birds were seen visiting the display grounds. Information on the behavior of males towards females is thus far less satisfactory than for *Manacus*.

I was unable to find many distinctions be-tween displays given to birds presumed to be females not ready for copulation and those given to birds presumed to be juvenile males. In both cases the owning male and the visiting bird are both aggressive, and the situation is usually con-fused. The owning male will land beside the vis-itor in the upright posture, and may then slide backwards towards it. The other may fly away and return, also landing in the upright posture. Both birds may dart back and forth, perform

about-faces, flick the wings, or turn away from the other and raise the wings and fan the tail.

But when the visitor was a (presumed) recep-tive female, there tended to be a more orderly sequence of display. Typically the males would start by repeated darting back and forth, utter-ing the thin "zit, zit," and would then change to display-flights. If the female went to a male's display perch, he would continue his display-flights, landing close beside her, inter-spersing them with the upright posture, back-ward-slides, and other elements of his display.

Copulation was seen only twice, and at-tempted copulation once. On April 26 a female came to the display perch of the male that was under observation and perched there in normal posture. He flew away and came back in dis-play-flight, landing immediately beside her. She remained still and he mounted. A little later the female returned to the same perch. The male flew in again in display-flight and landed beside her, but she then flew away. On April 29, during the all-day watch, a banded female flew to Male A's perch. He flew towards her from about two feet away, landed beside her in the upright pos-ture, and mounted. On August 29 Male B, in the course of confused mutual displays of the sort described earlier in this section, attempted to mount a female-plumaged bird that was very aggressive and was thought to be a juvenile male. On this occasion mounting was not preceded by a display-flight.

Very many times males were seen to fly in with display-flight and land close beside a fe-male, or presumed female, that had come to their display perches. Normally the female at once flew away to another perch. Flights to the female from a short distance, followed by the upright posture, were less often seen. Probably therefore the copulation sequence seen on April 26 is the most usual.

In *Pipra mentalis,* Skutch (1949) has described how the male lands straight on the back of the female after performing a circling flight. Although it is not easy to be sure of the details of the male Golden-headed Manakin's extremely rapid display movements, I had no evidence that they attempted to land straight on the female in this way.

The Daily Cycle of Display

An all-day watch was carried out on April 29, 1961, at the display ground that was under regular observation. All display-flights were counted from dawn to the time that display ended. From Text-fig. 3, which gives the results of this watch, it will be seen that after an early-morning outburst of display, activity fluctuated rather irregularly until 1545, when display ceased for the day. There was an especially intense bout of display between 1400 and 1500. The early-morning watches that were carried out weekly for over a year at this display ground showed that the time when the early outburst of display occurred was not constant. On some mornings there was little display between 0600 and 0700, and the main outburst was between 0700 and 0800. Later in the day, too, the times when display was most active were variable. In this respect the Golden-headed Manakin shows a less well-marked daily rhythm than *Manacus* (p. 75).

Text-fig. 3 also shows the times when females, or presumed females, visited the display ground. As would be expected, the presence of a female coincided with outbursts of display. Because of the difficulty of seeing the cryptically colored females unless they move, it was not easy to tell whether it was the arrival of a female that stimulated the males to display, or an outburst of display that attracted the females. It seems, however, that it is usually the arrival of a female that stimulates the males. Nevertheless outbursts of display certainly occur without any females being present, because, as in *Manacus,* the males at a display ground have a mutually stimulating effect on one another, so that when one starts to display others often follow and a general outburst results.

During the all-day watch, a record was kept of the periods of presence and absence of a male that had a display perch near the hide (Male A, mentioned above). This bird had occupied the same perch for at least 8 months; his habits and alternative perches were well known. His three nearest neighbors were all banded, but he was not. Between 0548, when he arrived, and 1700, when he was still present but display had long since ceased and the light was too bad for further

observation, he was present on or near his display perch for 88% of the time. His 43 absences were mostly very short, 29 of them being from ½ to 1½ minutes. It is probable that some of them were due to his merely flying for a short time to a perch that was out of sight. During one of the longer absences, of 5 minutes from 1612 to 1617, he bathed, as he returned with wet plumage and preened on a perch near his display perch. Excluding this absence, the time when he was away and could have been feeding was only 11% of the daylight hours.

An attempt was made to watch another male at the same time (Male B). His absences were of the same sort of length as Male A's, and they were often synchronized, as they occupied neighboring display perches, but it was not possible to obtain a complete record for this bird for the whole day. Less prolonged watching on many occasions gave no reason for supposing that the behavior of the males under observation on this day was in any way unusual.

The Annual Cycle of Display

Male Golden-headed Manakins display at all times of the year, except when they are moulting, but the intensity of display fluctuates somewhat throughout the season. During the regular early-morning watches at the main display ground under observation from August, 1960, to September, 1961, the intensity of display was measured by counting all the display-flights, a procedure which is rather easy as the display-flight is accompanied by a quite characteristic series of calls (p. 186). Text-figure 4 shows the intensity of display throughout a year, as measured during these watches. This figure also shows the season of moult in the two years 1960 and 1961, and the breeding season as far as it was ascertained, and thus provides a conspectus of the annual cycle for just over a complete year. It will be seen that display stopped during the moult in 1960, but not in 1961, when it was merely reduced. As mentioned above, the display in September, 1961, was not from the old established males, who had all begun to moult by then, but from newly arrived, probably recently moulted young males.

A more marked break in display occurred in December, 1960, and January, 1961, at exactly the same time as a break occurred in the display of *Manacus* (p. 82). Though there was evidence that food was temporarily short in the Arima Valley, where the observations were made, Golden-headed Manakins ceased displaying equally completely for the same period in an area of forest several miles away on the north side of the Northern Range, where food was
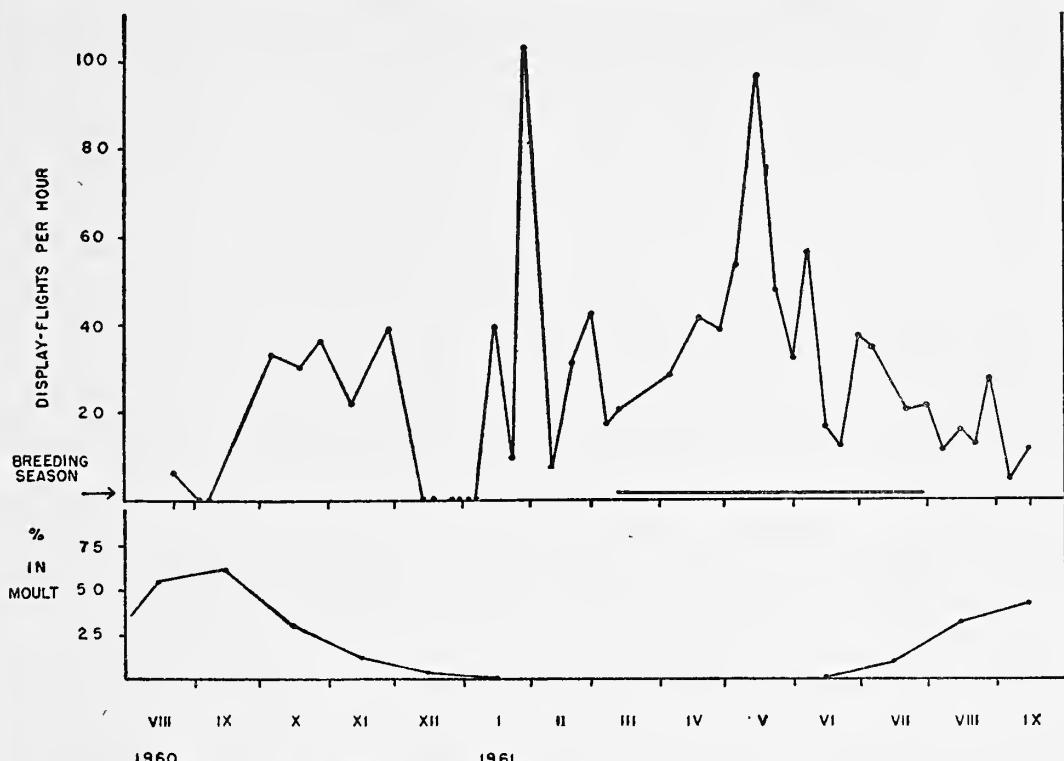
TEXT-FIG. 4. Annual cycle of display, breeding and moult, August, 1960, to September, 1961. Upper graph: intensity of display during early morning watches, based on number of display-flights per hour, and breeding season (horizontal line). Lower graph: moulting seasons, showing percentage of trapped adults undergoing wing-moult in each month.

abundant. The reason for the cessation of display was therefore not clear. Regular observations were not made all through December and January in other years, so breaks in display during that period could have gone undetected, but regular observations at a display ground of *Manacus* showed no comparable break in display in other years.

BREEDING

The Golden-headed Manakin's nest is typical of the family, a small, shallow cup slung in the fork between two horizontal twigs of a sapling or shrub, or the lower branches of a tree. It is thinly woven of brownish fibers and rootlets, and often has a few dead leaves bound into the bottom of the cup or hanging from the underside. The cup is usually so thin that the contents are partly visible from below. Those that were seen lacked the lining, made of the branching panicles of the melastomaceous herb *Nepsera aquatica,* that was found to be so characteristic of the nest of *Manacus* (p. 89).

Eight of the 15 nests that were found were between 4 and 8 feet above the ground. The other seven were from 10 to 35 feet. Probably

a much higher proportion of the nests are high up than these figures indicate, since high nests are much less easy to find. Since the low nests are not much less easy to see than the nests of *Manacus,* there seems no other way to account for the fact that only 15 were found compared with over 300 of *Manacus,* although the Golden-headed Manakin is the more abundant of the two species.

For 11 of the 15 nests, which contained eggs or young, the months of laying were as follows: March, 1; June, 4; July, 5; August, 1. The months of laying of the two nests recorded by Belcher & Smooker (1937) were January, and late March or early April. Four nests were found while being built, and so far as known no eggs were laid in them or, if laid, they were lost soon after; all these were in April and May. In addition, birds with incubation patches were trapped in May and July, and an egg-laying bird in March. It seems then that the breeding season extends from January to August, and that most clutches are laid in the latter half of this period —a breeding season substantially the same as that of *Manacus* (p. 82).

Few details of breeding were obtained, due to the high rate of nest failure. Four of the completed clutches consisted of two eggs, and one of one egg. The interval between the laying of the eggs was ascertained at two nests to be two days. One egg was found to have been laid between 1145 and 1545 hours. At one nest the incubation period was found to be 16 or 17 days. the fledging period was not ascertained, since none of the seven nests found before the time of hatching survived to the time of fledging.

FEEDING HABITS

Golden-headed Manakins feed in much the same way as Black and White Manakins; they pluck fruit on the wing, swallowing it whole on landing, and pick insects and spiders in flight from the twigs and foliage. The most obvious difference between the two species is that on average Golden-headed Manakins feed higher above the ground. Another probable difference is that they take relatively more insect food. Thus male Golden-headed Manakins at their display grounds regularly dart off for short sallies and pick food from the underside of leaves and from twigs, but Black and White Manakin males were never seen to do this. Probably there is more suitable insect food in the trees at the level at which Golden-headed Manakins display than near the ground where the Black and White Manakins have their courts, and probably also Golden-headed Manakins are the more fitted of the two species for this method of feeding, as they are far more agile on the wing.

Stomach contents of several birds were examined, but as most of them were trapped near places where fruit was abundant they yielded no valid information on this point. The stomach of a bird accidentally killed away from a trapping place contained remains of a spider 13 mm. long, a small beetle, a dipteran, an unidentified winged insect, an insect larva, and a few seeds and the skin of the berry of a melastomaceous tree.

Golden-headed Manakins are a little smaller than Black and White Manakins, and it seems that they cannot take such large fruits. Of the three largest fruits found to be eaten by *Manacus* (p. 92), 15-19 mm. long and 10-16 mm. in diameter, Golden-headed Manakins were seen to take only one (*Protium heptaphyllum*, 15 by 11 mm.).

Altogether, 445 records were obtained of Golden-headed Manakins feeding on the fruits of 43 species of plants (Table I). All but two of the plants were identified, at least down to generic level. All the fruits taken were small berries which were swallowed whole, with one exception: a bird was once seen picking pieces in flight from the large fruit of a species of *Henriettea* (Melastomaceae).

As for *Manacus* (p. 93), the Melastomaceae was found to be by far the most important family of food plants: 11 species were seen to be fed on, accounting for 63% of all the records. In number of species the Rubiaceae, with 6 species, came next, but very few records were obtained for each, and their total was only 2% of the whole. For *Manacus,* 14% of all records were from Rubiaceae. The difference is probably due in part to the higher level at which Golden-headed Manakins feed; the Rubiaceae with small fruit, likely to be most attractive to Golden-headed Manakins, (especially *Palicourea, Cephaelis, Gonzalagunia* and *Psychotria*),

TABLE I. FRUITS EATEN BY GOLDEN-HEADED MANAKINS IN THE DIFFERENT MONTHS

Species	Numbers of records in different months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
MORACEAE												
Ficus citrifolia		1										
Ficus clusiifolia		4	5	3	5	1				3	7	
URTICACEAE												
Trema micrantha					2							
NYCTAGINACEAE												
Pisonia eggersiana									3			
LAURACEAE												
Ocotea canaliculata			6	1								
Phoebe elongata				2	1							
BURSERACEAE												
Protium heptaphyllum									3			

TABLE I. FRUITS EATEN BY GOLDEN-HEADED MANAKINS IN THE DIFFERENT MONTHS *(continued)*

Species	Numbers of records in different months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
EUPHORBIACEAE												
Alchornea triplinervia				4								11
Hieronyma caribaea		2								2		
Maprounea guianensis											5	
Sapium aucupariuin								4				
AQUIFELIACEAE												
Ilex sp.												1
TILIACEAE												
Sloanea laurifolia			5									
Sloanea stipitata					3							
DILLENIACEAE												
Davilla aspera					1							
Doliocarpus dentatus					5	4						
Pinzona calineoides				1								
FLACOURTIACEAE												
Laetia procera				5		1					2	
MYRTACEAE												
Myrcia leptoclada			2									
MELASTOMACEAE												
Henriettea sp.											1	
Miconia affinis						10	7	12	1			
Miconia chrysophylla					6	1						
Miconia guianensis	18	8	1	4							1	8
Miconia kappleri	4									4	23	36
Miconia multispicata		2	10	7	3							
Miconia myriantha				1						3	24	
Miconia prasina					1	20	4	25	11			
Miconia punctata	3										4	
Miconia splendens					2							
Miconia tomentosa					2	4						
Miconia sp.										3	6	
ARALIACEAE												
Didymopanax morototoni											13	32
VERBENACEAE												
Aegiphila integrifolia												5
PHYTOLACCACEAE												
Phytolacca icosandra					1							
SOLANACEAE												
Cestrum baenitzii							2					
RUBIACEAE												
Cephaelis muscosa							1					
Isertia parviflora										1		
Malanea macrophylla		1										
Palicourea crocea	1											
Psychotria inundata										3		
Psychotria marginata												1
COMPOSITAE												
Wulffia baccata									1			
Unidentified vine (1)							1					
Unidentified vine (2)												2
Number of species	4	5	6	9	12	7	5	5	3	6	9	8

are shrubs or low trees, while the larger rubiaceous trees and vines which are at the level where Golden-headed Manakins mainly feed (*Amaioua, Coussarea, Lacistema, Malanea*) have larger fruits which are at or near the upper limit of size for Golden-headed Manakins.

Of the other families, the Euphorbiaceae, Moraceae and Araliaceae were the most important. Four species of Euphorbiaceae contributed 6% or all the records, and two species of *Ficus* (Moraceae) 5%. Apart from some of the melastomes, the greatest number of records from a single tree species came from *Didymopanax morototoni* (Araliaceae), which contributed 10% of the total.

The number of fruit species found to be eaten in each month varied from 3 in September to 12 in May. Most different kinds of fruit were found to be eaten in the months April-June and November-December. Though the species involved are partly different and the total numbers smaller, this is the same picture as was found for *Manacus* (p. 93) and suggests that the availability of fruit shows a double peak in the year, of which the first, major peak comes in the middle of the breeding season.

PLUMAGES, MOULTS AND COLOR OF SOFT PARTS

Moults

The moults follow the same course as in *Manacus* (p. 82). There is a slow post-juvenal moult in the first year of life, involving the head and body, lesser wing-coverts and some inner secondary major coverts. Most of the birds undergoing this post-juvenal moult were trapped in the months August-January. The next moult, to adult plumage, is complete and takes place in the second summer and autumn, Thereafter there is an annual moult in the months August-November.

Fifteen birds were trapped while moulting from juvenile to adult male plumage. As was found in *Manacus* (p. 85), these birds on average moulted earlier than the adult males (Text-fig. 5).

Four birds were trapped twice in the course
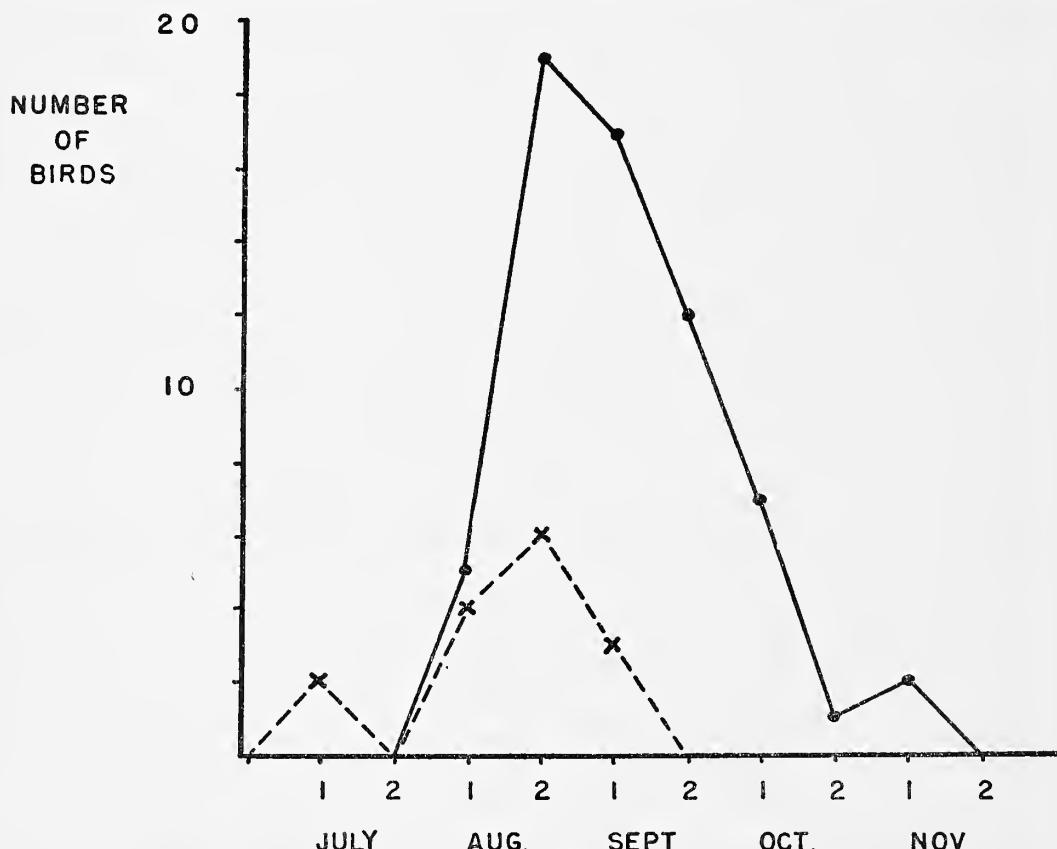
TEXT-FIG. 5. Moulting seasons of old and young males. Solid line: fully adult males trapped in moult. Broken line: males trapped while moulting from juvenile to adult plumage.

of a single moult. The amount that the moult of the wing-feathers had progressed between the two captures showed that the complete moult must last about 90 days, a figure similar to that obtained for *Manacus* (p. 85). Four birds trapped while moulting in two or three different years showed slight annual variations in the timing of their moult. In the population as a whole, the season of moult did not vary much in the four years for which data were obtained (Text-fig. 6), except that it ended earlier in 1958 than in 1959 and 1960.

Plumages

Female Golden-headed Manakins regularly have a few male-type feathers in the head and body plumage, and in those that were trapped more than once the number and distribution of these feathers remained much the same from one year to the next. Juvenile males also often have a few adult male feathers in the head and body, so that on the basis of plumage they can-

not be separated from adult females. A small proportion of the adult males had some female-type feathers in the plumage. Usually only a few were scattered here and there, but two adult males had the plumage of the underparts almost entirely female, and many female-type feathers elsewhere in the plumage; and one had all the feathers of the head and body of partly male and partly female color. A fourth had a completely mixed plumage, with male and female-type feathers intermingled in the head, body and wing. This bird was trapped four times over a period of just over two years, and its plumage remained exactly the same.

Five birds in female plumage and one adult male had partially albino plumage. In all of them, the dark pigment was lacking in some of the flight-feathers, which were white or pale yellow.

In addition to these variations, the general body color of birds in female plumage varied
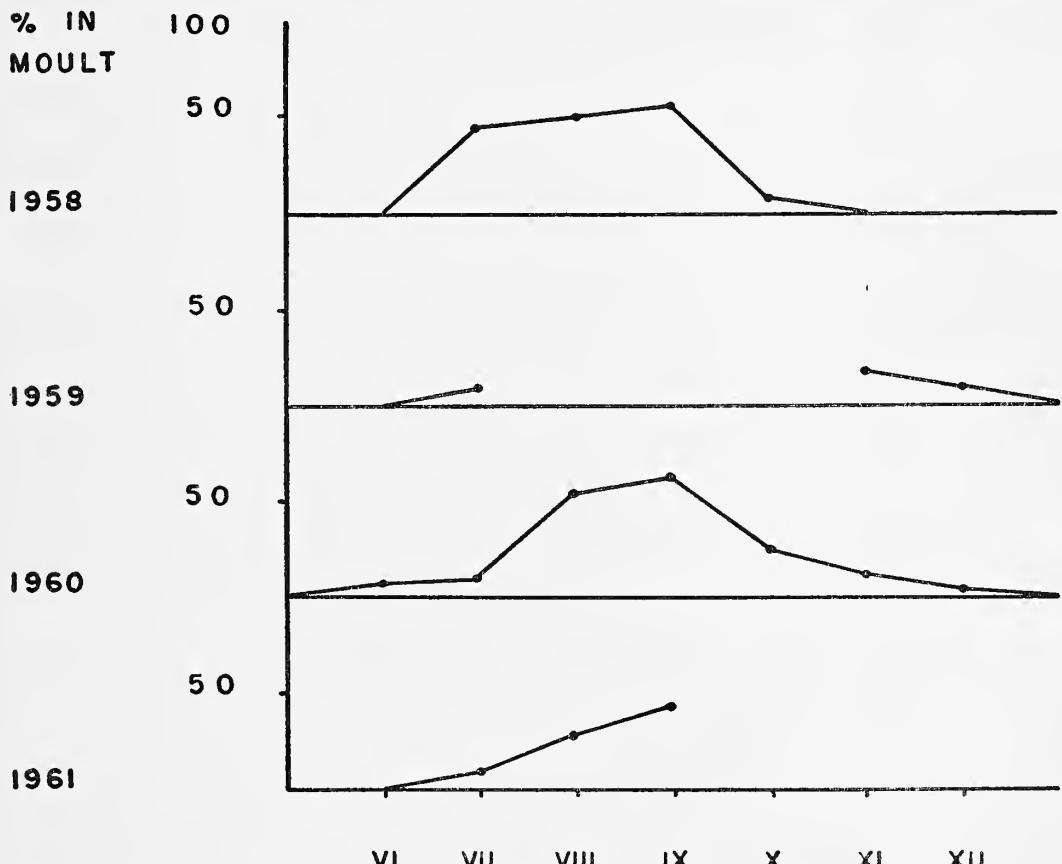
TEXT-FIG. 6. Moulting seasons, 1958-1961. Each graph shows the percentage of trapped adults undergoing wing-moult in each month, based on the following totals: 1958, 122; 1959, 104; 1960, 254; 1961, 124. Gaps in 1959 and 1961 indicate periods when no observations were made. (A single bird moulting in March, 1961. is not shown).

considerably, from the usual olive-green to a paler, yellower green. Several birds had a pale crown-patch of the same shape as the adult male's golden cap.

Variation in plumage is much greater in the Golden-headed Manakin than in *Manacus,* in which only three slight abnormalities of plumage were found in the 275 individuals caught in the study area. The reason for the difference is quite obscure, but it may be noted that it applies also to the color of the iris, beak and legs, as described in the following sections.

Eye-color

The iris of adult males is white. Only one exception was found to this rule: the male with mixed plumage, mentioned above, had its iris mainly white but bordered with gray-brown around the pupil. In birds of female plumage the iris is variable, ranging from gray-brown or seal-brown (as in juveniles) to white through various intermediates in which it is blotched, dotted, mottled or clouded with varying amounts of white.

It has previously been assumed (e.g., Conway, 1959) that birds in female plumage with some white in the eye are juvenile males. However, analysis of the eye-color of the birds that were trapped more than once showed that the situation is far from simple, and in particular, that birds with intermediate eye-colors are more often females than juvenile males.

Twenty-seven known females were retrapped aften an interval of 8 months or more. In 19 of them, the iris was dark when they were first trapped. In 13 of these, the iris remained dark after intervals of 8 months to 2½ years; in the other 6, the iris was spotted or flecked with white when they were next trapped, after intervals of 8 months, 1 year, 1 year, 2 years, 3 years and 3 years. Eight known females had varying amounts of white in the iris when they were first trapped. In four of them the eye appeared unchanged when they were next trapped, after intervals of 9 months to 1 year 8 months; in two the white spots had enlarged, 1 year 8 months and 2 years later; and in two the white spots later disappeared. One of these two, trapped four times, had small white spots which remained for a year, then disappeared four months later. The other, trapped three times, had large white spots when first trapped; five months later it had small spots, eight months after that the eye was dark, and 2 years and 4 months after that it again had a partially white iris. On this last occasion it also had 2 white flight-feathers in one wing and one white feather in the other wing; previously its plumage had been normal.

There must be a greater tendency for white spots to appear and increase in the course of a female's life than to decrease, as they all start life with dark eyes; but the amount of white does not usually increase indefinitely. This is shown not only by the evidence given above, but also by the fact that no bird that was definitely known to be female had an all-white eye. Twenty birds were trapped in female plumage, with an all-white eye. Three of them were later found to be males, and eight others probably were, as they were trapped at the season when the eye-color of juvenile males changes to white (May-July). Thus not more than 17, and probably less than half that number, of the approximately 300 females that were trapped could have had white eyes.

Nine males were trapped in juvenile plumage and then retrapped after moulting to adult male plumage. Four of them, first trapped in their first November, December and January (2), all had dark eyes (as had two juvenile males collected in October). Of the other five, one was trapped in the April before its moult and had a light gray, slightly mottled iris; one in May had the iris gray, clouded with white; and three in June all had the iris white, one of them being still rather dull. In addition to these birds that were trapped before and after their moult to adult plumage, fifteen young males were caught while moulting to adult plumage. In 13 of them the eye was fully white, and in the other two it was white, faintly clouded with gray.

Thus the eye-color of these males changed to white in the last few weeks before they moulted, the intermediate stages being uniform gray, or clouded or faintly mottled with white. None had the iris dark with white spots, as in females.

Color of Beak and Legs

The upper mandible is straw-yellow in adult males and horn-brown in females and young birds; the lower mandible is yellowish in all birds, paler in males than females. Within the sexes there is some individual variation, and in adult males seasonal variation too was found, the color of the upper mandible becoming darker at the time of the moult.

The color of the legs varies, from the usual flesh-pink to dull grayish pink and even occasionally blue-gray. It seemed probable that the birds with the darkest, grayest legs were mainly young birds, but this was not proved.

SUMMARY

The Golden-headed Manakin, *Pipra erythrocephala,* was studied in an area of primary and secondary forest in the Northern Range of

Trinidad. On the study area it was the most abundant forest bird, with an adult density in excess of one bird per acre. The annual mortality of adults was estimated to be about 10%.

The males display at communal display grounds, where each occupies a display perch 20-40 feet up in a tree. Display grounds persist year after year in the same places.

The various display movements are described and figured. The most conspicuous display consists of a rapid swooping flight to the perch, followed by a backward-slide, with associated wing and tail movements. Copulation follows immediately after a display-flight.

Neighboring males are potentially hostile to each other, but little overt aggressiveness is shown. Pairs of males spend much time sitting side by side mid-way between their display perches.

The males spend about 90% of the daylight hours at their display grounds, and are normally present at them all through the year except when they are moulting.

The breeding season extends from January to August. The nest, a thinly woven cup slung in the fork between two horizontal twigs, is placed from 4 to 35 or more feet above the ground. None of the nests found survived to fledging.

The food consists of berries and small invertebrates, taken on the wing. Observations showed seasonal variations in the amount of fruit available, with peaks in April-June and November-December.

Moults and plumages are described. There is a slow post-juvenal moult in the first year, followed by a complete moult in June-September. Subsequent annual moults occur a little later, in July-November.

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APPENDIX

WEIGHTS AND MEASUREMENTS

As for *Manacus* (p. 102), birds were placed in a cloth bag and weighed immediately after being trapped. A spring balance accurate to 0.5 gm. was used.

Weights have been used only for birds of known sex. A very large number of weights of birds in female plumage, which were never retrapped and so could not be sexed, have been discarded.

Similarly wing-lengths are given only for birds of known sex.

Wing-lengths

Wing-length (mm.)	Adult males	Juvenile males	Females
62			1
61			4
60	2	5	15
59	13	4	28
58	42	7	14
57	79		4
56	64	1	1
55	30		
54	5		1
53	1		
52	1		
Totals	237	17	68
Means	56.7	58.7	58.9

Weights of Adult Males

Weight (gm.)	Months						All months
	I-II	III-IV	V-VI	VII-VIII	IX-X	XI-XII	
17	1						1
16						1	1
15				3	3	2	8
14.5		2		2	4		8
14	1	1	1	5	11	6	25
13.5	4	3	3	11	12	8	41
13	4	5	16	11	13	7	56
12.5	15	10	9	10	9	11	64
12	10	6	11	7	8	9	51
11.5	5	4	6	5	2	7	29
11	2		2			2	6
10.5					1		1
Totals	42	31	48	54	63	53	291
Means	12.5	12.6	12.5	13.0	13.2	12.8	12.79

Weights of Juvenile Males

Weight (gm.)	All months
13.5	2
13	2
12.5	3
12	2
Total	9
Mean	12.7

Weights of Females

Weight (gm.)	Months						All months
	I-II	III-IV	V-VI	VII-VIII	IX-X	XI-XII	
16.5		1					1
16			3	5		3	11
15.5		1	3	8	2	1	15
15		1	5	13	5	5	29
14.5	3	5	3	11	13	3	38
14	9		5	4	16	10	44
13.5	9	3	3	5	9	5	34
13	6	1	3	5	6	5	26
12.5	2	1	2	1	2	4	12
12	1			1	2		4
Totals	30	13	27	53	55	36	214
Means	13.5	14.3	14.4	14.6	13.9	14.0	14.12

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The Natural History of the Oilbird, *Steatornis caripensis,* in Trinidad, W. I. Part 2. Population, Breeding Ecology and Food[1,2,3]

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(Plates I-IV; Text-figures 1-4)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest preserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction of the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe, Zoologica. 1952, 37 (13: 157-184.]

THE TRINIDAD POPULATION

THERE are at present eight known Oilbird colonies in Trinidad, in caves ranging from sea level to about 2,500 feet (Text-fig. 1, Table I). The four best known have been the subject of numerous accounts, ornithological and popular (*e.g.,* Kingsley, 1871 (Huevos); Chapman, 1894 (Huevos); Cherrie, 1907 (Aripo "Main Cave"); Roosevelt, 1917 (Oropouche); Williams, 1922 (Arima, Oropouche); Hollister, 1926 (Arima, Huevos); Myers, 1935 (Arima); Sanderson, 1940 (Aripo "Main Cave"). I have found no published account of La Vache cave and the smaller Aripo

caves. In addition, at least five small colonies, four of them in sea caves, have been exterminated in recent years as the result of raids by fishermen and others. These also are listed in Table I. It is rather unlikely that any important colony remains undiscovered, but not impossible that in the limestone of the Aripo massif there may be small undiscovered colonies. Some of this country, which is honeycombed with small caves, is difficult to penetrate and not much visited.

I was able to visit all the known colonies, some of them several times, and made an attempt to assess the present adult population (Table I). Direct counting of all the adults is impossible in most of the caves; instead, it is necessary to count all the nests which appear to be occupied, count all the birds that can be seen perched on nests and ledges, estimate the number of birds flying about, and from these figures assess the number of birds present. I think it unlikely that the estimated total of 1,460 adults is out by more than 500 either way.

Such a small population of a very specialized bird is highly vulnerable, and indeed the extinction of five colonies is evidence that the Trinidad population has been reduced in recent times. None of these exterminated colonies can, however, have been very large. The larger Trinidad colonies, like those in Venezuela, have persisted for years in spite of constant exploitation by man. Though their numbers have probably been reduced, they are certainly under no immediate threat. As long as the forest remains, which provides the Oilbirds' food, the steady harvesting of a proportion of the young birds, though deplorable, is no danger to the survival of the
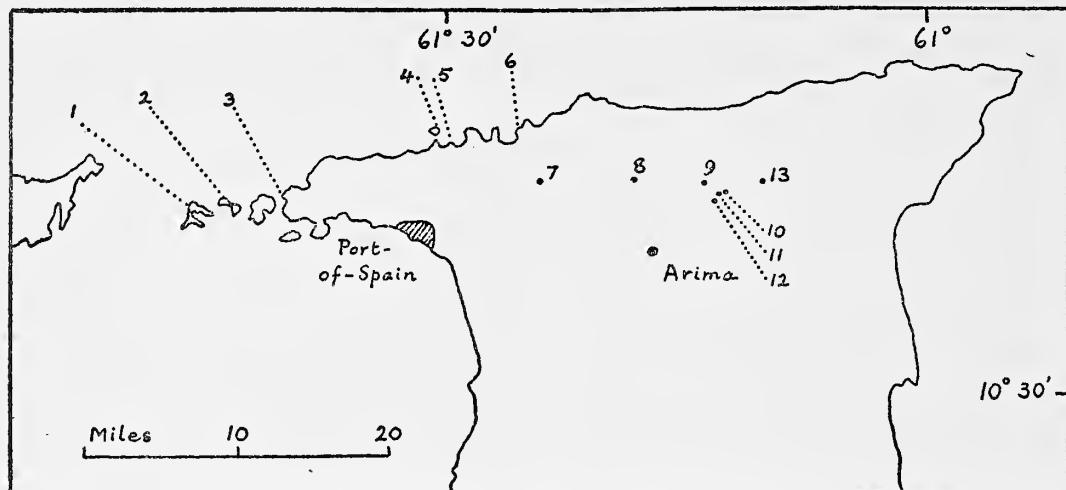
TEXT-FIG. 1. Trinidad Oilbird colonies. **1**: Chacachacare (extinct). **2**: Huevos. **3**: L'Ance Pawa (extinct). **4**: Saut d'Eau (extinct). **5**: La Vache. **6**: Maracas Bay (extinct). **7**: Acono (extinct). **8**: Arima gorge. **9**: Aripo main cave. **10**: Aripo well cave. **11**: Aripo middle cave. **12**: Aripo small cave. **13**: Oropouche. For further details see Table I.

species. A more real danger may come from the mounting pressure of the human population on the surviving areas of forest. It is to be hoped that future governments will both conserve the forests and protect the birds.[4]

The Arima gorge colony is known to have fluctuated greatly. During the present study there have usually been 25-30 adults present, and the number of breeding pairs in the years 1957-62 has been as follows: 11, 13, 9, 9, 8, 11. The breeding population cannot in fact rise much above the 1958 figure, as there are not more than 15 or 16 suitable nest-sites. In September, 1959, the colony was raided by a poacher; at least eight adults were killed and for some weeks the cave was almost deserted of birds. Gradually the survivors returned, until by December, when breeding began again, there were 14 birds, and a little later 21 birds were present. At various times in the past the numbers reported have been very low, probably as a temporary result of the same cause. Clearly this colony could easily be exterminated by steady persecution.

THE ANNUAL CYCLE OF BREEDING AND MOULT

There has hitherto been no exact information

on the Oilbird's breeding season, for either Venezuela or Trinidad. Most naturalists have visited the colonies in the first half of the year, especially from March to May when the birds are known to be nesting. There is a widespread belief in Trinidad that May is the month to collect young birds; luckily for the birds, this is only partly true. May is a good month, but other months may be equally good.

Table II shows that in the five years 1957-1961 clutches were started in the Arima colony in every month except October and November, with 87% of the total in the six months December-May. There is a distinct annual breeding season, with a very variable start. In three years the main period of laying started in December, in one year in January (1962, for which records were obtained up to the end of May), and in two years in March. In each year several nests started within a week or two of each other, and the later nests in the following few weeks. There seems no doubt that some kind of mutual stimulation is involved in this synchrony.

Limited information on other colonies has indicated breeding seasons similar to that at the Arima gorge colony. But there are not many caves where it is at all easy to inspect the nests, and information is very incomplete. Also, these other caves are regularly disturbed by poachers, so that the normal breeding season may be obscured. Thus visits to La Vache cave in 1958, the Huevos cave in 1959 and the Aripo Well cave in 1960 and 1961 all indicated a breeding season similar to that at the Arima gorge in the

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[4]Oilbirds are protected by law in Trinidad, but the law is not enforced and would be difficult to enforce. The Aripo, La Vache and Huevos caves are still regularly raided. The Oropouche cave is on private land and the owners are trying to protect it, but it is not difficult for poachers to enter unobserved and they apparently still do so. The Arima gorge colony is also on private land and is protected by the owner.

same year; but on another visit to the Aripo Well cave in March, 1959, when breeding was just beginning in the Arima gorge (Table II), six of the ten nests whose contents could be seen contained young of a size that indicated egg-laying in December and January.

Intervals between Broods and Sequence of Broods.—The limited evidence suggests that undisturbed pairs retain their nests year after year. One banded bird was seen on the same nest in three successive years, and another in two successive years. Unfortunately the raid on the cave in September, 1959, when a number of adults were killed, probably including two banded ones, put an end to these observations, but they suggest that successive clutches in the same nest are normally laid by the same female, and this has been assumed unless there was evidence to the contrary.

On this assumption, an analysis has been made of the intervals between the ending of one nesting attempt and the laying of the first egg of the next clutch, excluding intervals spanning the time of the raid on the cave. Table III gives the 47 intervals that are available for analysis. It will be seen that nesting attempts that ended in failure in the months December-May were nearly all followed by a new clutch after intervals ranging from 19 to 75 days (mostly 19-33 days). Those that ended in failure in the months June-October were nearly all followed by intervals of several months, during which the pair concerned probably moulted (see next section), leading to re-laying in the following breeding season. The intervals following successful nesting attempts were less consistent. Those that ended in the months April-August were followed either by intervals of less than 34 days, leading to a further attempt in the same breeding season, or by long intervals of several months during which the pair probably moulted, leading to re-laying in the next breeding season. Among

TABLE I. PRESENT COLONIES OF OILBIRDS IN TRINIDAD AND THEIR POPULATIONS

Colony	Population
Oropouche cave	200
Aripo caves	
"Main cave"	400
"Small cave"	10
"Middle cave"	140
"Well cave"	80
Arima gorge (Spring Hill cave)	30
La Vache cave	300
Huevos cave	300
	1460

Notes on Colonies

Present colonies:

Oropouche cave. Extensive limestone cave formed by stream flowing out of hillside through narrow entrance. Nests from half-light near entrance to total darkness of furthest large chamber. Population based on count of birds leaving the cave in the evening (Part 1, p. 33).

Aripo main cave. Large limestone cave with wide entrance and stream flowing down into cave. Most nests in subdued light near entrance. Population estimate based on adults seen in cave and occupied nests.

Aripo small cave. Small limestone cave with dry floor; nests in subdued light. Counts on three visits: 12, 12 and 10 birds.

Aripo well cave. Dry limestone cave with top entrance. Some nests in almost full daylight, possibly even receiving a little sunlight. Population

assessment based on counts of birds on nests and ledges.

Arima gorge. Partially covered-over gorge with stream flowing through. Adult population usually 25-30.

La Vache cave. Sea cave. Single large vaulted chamber about 75 feet high, with semicircular entrance 20 feet high. Assessment based on estimates of flying and perched birds on three visits.

Huevos cave. Sea cave. Single long chamber about 100 feet high, with entrance 15 feet high. Assessment based on direct count of 230 perched birds, with allowance for some flying and others perched out of sight.

Extinct colonies:

Chacachacare. Small sea cave on west side of island. Remains of nests and a few dry seeds found by Dr. T. H. G. Aitken, November, 1958. No further details known.

L'Ance Pawa. Sea cave about quarter of a mile to seaward of L'Ance Pawa Bay. Contained about a dozen or 20 birds in 1918 (Williams, 1922). Deserted in 1960, and no sign of recent occupation.

Saut d'Eau. Open sea cave on northeast side of Saut d'Eau Island, with a short tunnel through the cliffs. According to local information, occupied ten or twenty years ago but found deserted in 1960 and apparently had been for several years.

Maracas Bay. Small sea cave a short distance east of Maracas Bay. Deserted in 1957; some remains of old nests found. According to local information, had been occupied some 15 years previously.

Acono cave. Gorge in Acono Valley. Occupied in nineteenth century (Wall & Sawkins, 1860); deserted in 1918 (Williams, 1922).

TABLE II. BREEDING SEASONS OF OILBIRDS IN THE ARIMA GORGE COLONY
Numbers of clutches started in each month

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1957[1]	—	—	4	5	2	—	2	1	1	—	—	4
1958	2	1	8	1	4	2	—	—	—	—	—	—
1959	—	—	3	3	3	—	1	2	—	—	—	1
1960	3	4	—	1	1	—	—	—	—	—	—	3
1961	2	2	1	—	1	—	—	—	—	—	—	—
1962[2]	5	1	4	3	1							
Totals	—	—	—	—	—	—	—	—	—	—	—	—
1957-61	7	7	16	10	11	2	3	3	1	—	—	8

[1]Visits did not start until March 20, 1957. There were then no nests that could have started in January or February, but it is possible that some had started and already lost their contents by March 20.

[2]The 1962 records were obtained by Mr. J. Dunston, who inspected the cave regularly from the end of September, 1961, to June, 1962, after my own observations had ceased. These extra 14 nests are not included in the analyses of clutch-size, breeding success, etc., given elsewhere in this paper.

the short intervals there were two cases of the first egg of a new clutch being laid, in one case about 13 days before, and in the other case at about the same time as, the departure (from the same nest) of the last young of the previous brood. Those nesting attempts that ended successfully in the months October-January were followed mainly by intervals of intermediate length, leading to re-laying early in the following breeding season.

A complete nesting cycle, from the laying of the first egg to the fledging of the last young, lasts about five months (Part 1, p. 39). Thus with a short interval between broods it is just possible to rear two broods in a year, and this was in fact achieved by three pairs during the present study. One of these reared two broods between early December and the following October, having also reared a brood between April and September of the previous year. Thus they reared three broods in eighteen months. After the last they had an interval of 13 months before the next clutch was laid. Another pair, having completed the rearing of two broods between December and October, laid a new clutch in December, after an interval of 49 days, certainly not long enough for the moult. This brood was also successful and fledged in the following May, so that three broods were again reared in 18 months. There was then an interval of eight months before the next clutch was laid in the following January. The third pair reared two broods between March and the following January; they then had a gap of five months before the next clutch was laid, in late May but this failed and the sequence was broken. The data are insufficient for a proper analysis, but they suggest that pairs breeding successfully can rear two broods in a year only every second or third

year. Discussion cannot be taken any further without considering the relation between breeding and the moult.

The Moult.—At every visit to the colony, all moulted flight-and tail-feathers were collected. Most of the moulted feathers are dropped outside the cave, presumably during feeding, but enough are dropped inside the cave to give an indication of the amount of moulting taking place in the colony. Nearly all were found on the slopes below the nests and could not be allocated to known nests.

Moulting takes place in every month of the year, but there is a well-marked seasonal variation. There is most moulting in the six months June-November (72% of all moulted feathers being found in these months) and least moulting in the six months December-May. Thus there is an inverse correlation between egg-laying and moulting, but nevertheless enough moulting takes place in the months December-May to make it very likely that some birds at least undergo moult while breeding. Examination of specimens suggests the same. Thirty-five dated Trinidad specimens have been available for examination (13 in the American Museum of Natural History, 11 in the British Museum and 11 trapped or collected during this study). Twenty-six were collected in the months January-May, the main egg-laying period, and 16 of them were undergoing moult of the primaries. The remaining nine were collected in July-October, and seven of them were moulting their primaries.

The sequence of moult is variable and sometimes irregular. Of 29 Trinidad specimens which were in wing-moult (those mentioned above and some undated specimens), 14 appeared to be undergoing a normal replacement of the primaries from the inner end of the row out-

TABLE III. INTERVALS BETWEEN BROODS
(Length of time between ending of one nesting attempt and laying of first egg of next clutch)

Month in which nesting attempt ended	Intervals of less than three months (in days)	Intervals of more than three months (in months)
January	—	5
February	*23, 25*	—
March	*24*	—
April	—	8½
May	0, **19**, **19**, **20**, *23*, 33, *47*, **65**, *75*	9
June	*44*	6, 6, 6½, 7, 7, 7, **9**
July	—	6½, **7**, 8, 8½, 9½
August	*−3*, 25	5, 5, 6½, 7, 7½, 8
September	76, 78, 84	3
October	49	4, *5½*, 7, 15
December	*24, 72*	—

NOTE: Figures in ordinary type: previous nesting attempt successful. Figures in *italic* type: previous nesting attempt ending in loss of eggs. Figures in **heavy** type: previous nesting attempt ending in loss of young.

wards. Four other birds showed a similar condition, except that the moult of one wing was one or two feathers in advance of the other. The remaining 11 birds showed more complex or irregular conditions. In six, one wing was moulting but not the other, and in one of these moult was occurring in two separate places in the row. The remaining five all showed moult in two separate places in the row in at least one wing, and in one bird three feathers in the same wing (primaries 1, 6 and 9) were all in various stages of growth.

The most reasonable explanation for the presence of growing feathers at two separate places in the row seems to be that a second moult of the primaries had started before the previous one was complete. The clearest case was that shown in Text-fig. 2a, where a second moult had apparently started when the previous one was about half completed. Another bird was similar, except that the two wings were at slightly different stages. A third case, shown in Text-fig. 2b, was the bird mentioned later in this section, which was caught twice while moulting, and another showed an exactly similar condition, including the asymmetry between the two wings, except that the moult was at a slightly later stage. Alternatively, it may be that the moult sometimes starts simultaneously at two "foci" and proceeds outwards from these two points. Parallels for both conditions can be found in other birds; *e.g.*, overlapping successive moults in boobies (Dorward, 1962), multiple

"foci" in birds of prey (V. & E. Stresemann, 1960).

The length of time needed for a complete moult must be several months. Examination of specimens showed that altogether there were only seven instances of two adjacent primary feathers growing, as against 51 instances of a single feather growing, in many cases nearly full-grown. Thus (unless moult starts at two foci) replacement of the whole series of ten primaries must on average take nearly ten times the length of time needed for the growth of a single feather. One individual of the Arima gorge colony was caught twice during the same moult, at an interval of exactly four weeks. Of the three feathers which were one-quarter grown on April 21, one was full-grown and the other two nearly full-grown on May 19 (Text-fig. 2b). If this bird was typical, more than ten months would be needed for a complete moult of the primaries, and even with moult starting from two foci not less than six months would be required.

Table III shows that several of the long intervals between nesting attempts were of less than six months, so that for these birds the moult must surely have overlapped the previous or subsequent nesting cycle, and since six months is probably an underestimate for the period of the moult, others may have done so as well.

The possibility must be considered that the rate of moult is variable; in particular, that it is faster during the off-season and slows down
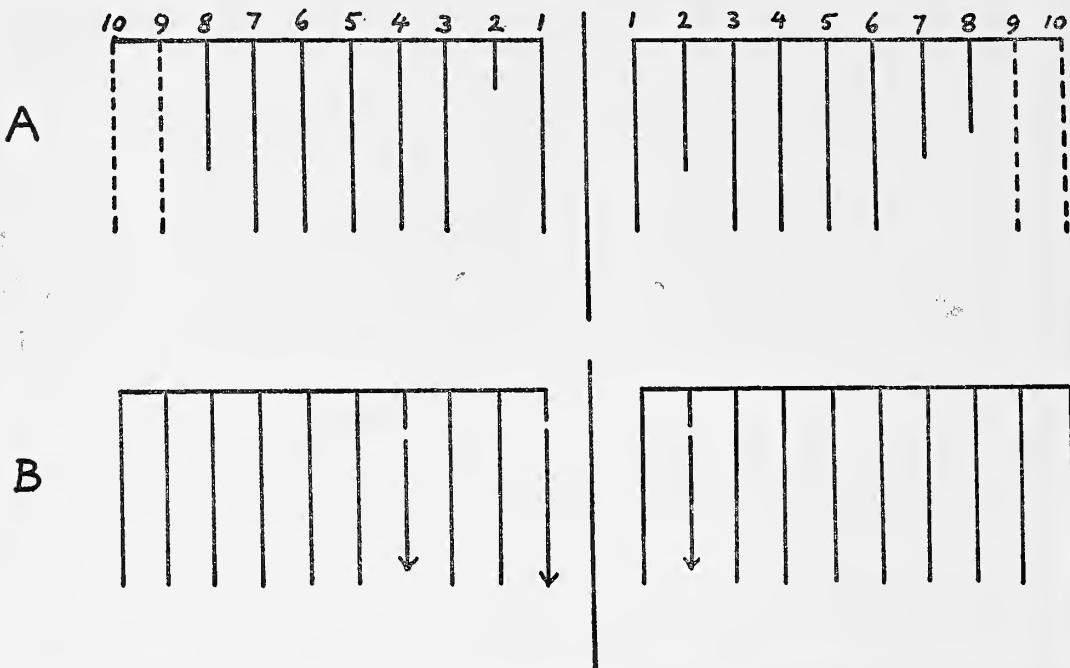
TEXT-FIG. 2. Stages of primary moult in two Oilbirds. The ten primaries are shown diagrammatically from above, as follows: solid lines, complete or growing feathers, not recognizably old; broken lines, recognizably old feathers; arrows, amount grown between first and second captures (see text).

when the bird is breeding. Even without any connection between the timing of the onset of the moult and the breeding cycle, such a variation in rate of moult could account for the fact that moulted feathers were found in all months, but nearly three times as numerously in the months July-November as in the months December-May.

To summarize, the data show that the moult mainly occurs in the six months June-November, coinciding with the long intervals following nesting attempts that end in those months, and the evidence suggests that the moult of each individual lasts for several months and may overlap the nesting cycles. The possibility of variation in rate of moult according to the state of breeding must also be borne in mind. More definite conclusions are not warranted on the present evidence. Far more captures of birds with known nesting histories would be necessary to establish the exact relationship between breeding and the moult. Since it was found that the capture of adults had a disturbing effect on the whole colony, it was not practicable to obtain more than these fragmentary data.

CLUTCH-SIZE

Clutches numbered from one to four eggs. Of the four one-egg clutches, three were laid by the same bird, perhaps a young bird breeding for the first time (see next section). The mean size of the 59 completed clutches was 2.7 eggs (Table IV).

Mean clutch-size decreased in the course of the breeding season from just over three to two eggs, 10 of the 11 clutches of four eggs being laid in the early part of the breeding season (December-March). It will be shown later that most food is available in the months March-June (Text-fig. 4), the period when most of the young from the early clutches are in the nest. It is reasonable to suppose that the seasonal variation in clutch-size may be adapted to the seasonal change in the food supply, as has been found for many north-temperate birds (*e.g.*, Lack, 1954).

BREEDING SUCCESS

In the five years of observation, nearly half of the nesting attempts produced flying young. There were 68 nesting attempts (in which at least one egg was laid); 45 of these reached the hatching stage (and four more may have done so, the eggs or young disappearing around the hatching time); and of these, 31 reached the fledging stage, producing a total of 60 young. The earlier nests were more successful than the later ones, 21 out of the 38 nests starting in the months December-March producing fledged

TABLE IV. CLUTCH-SIZE

| | Number of eggs in clutch | | | | Mean clutch-size |
	1	2	3	4	
December		1	2	3 }	
January	1	2	1	3 }	3.1
February		1	4	2 }	
March	1	7	6	2 }	2.7
April		4	5	}	
May	1	5	2	1 }	2.4
June		2		}	
July	1	1		}	(2.0)
August			1	}	
Total (59)	4	23	21	11	2.7

young, compared with 10 out of the 30 starting in April-September. These figures are too small to be convincing of themselves, but the difference is probably real and due to the nesting behavior becoming less efficient as the season advances. Thus there were seven instances of eggs being deserted or lost soon after laying in the months April-September, and only two in the months December-March. There was an unbroken run of successes at only one nest, probably kept by the same pair throughout the period. At this nest there were five successful nestings, producing nine flying young. (This was one of the nests mentioned earlier, in which three broods were reared in 18 months). No nest had an unbroken run of failures, though some nearly did. In some cases a sequence of failures

probably represented the first nesting attempts of a young pair. Thus at one nest four failures were followed by two successes, the clutch-sizes for this sequence being 1, 1, 1, 2, 4, 3.

Table V shows the fate of the 171 eggs laid. For nine clutches there was uncertainty as to the number of eggs laid, due to the disappearance of the clutch during laying. In these cases the greatest number known to have been laid has been counted. For others there is uncertainty as to the number of young hatched, owing to the disappearance of an egg (or young) at about the time that hatching was due. As unhatched eggs were known in several cases to remain in the nest long after the others had hatched, and several young were known to have died soon after hatching, it is likely that in most of these uncertain cases the eggs did in fact hatch.

The causes of egg failure were various. Sometimes an adult may kick off an egg as it flies from the nest. This was seen to occur once and it probably accounted for several other egg losses. Three times nests were flooded by water seeping through cracks in the rock during very wet weather and the eggs were chilled and eventually thrown out by the owners. Many other egg losses were unaccounted for; a few of these may have been caused by the crabs (*Pseudothelphusia garmani*) which occasionally walked over the nests and probably attacked the young.

Nearly 60% of the young known to have hatched reached the flying stage. As with eggs, the causes of failure were mostly unknown. Most died in the early stages, and it is probable

TABLE V. HATCHING AND FLEDGING SUCCESS

Eggs/young present		Losses	
Eggs laid	171	Deserted without being incubated	2
		Flooded; thrown or washed out	7
		Kicked off by adult	1
		Used for egg-white sample	1
		Disappeared before possible hatching date (cause unknown)	31
Eggs remaining at hatching time	129	Infertile	7
		Deserted	1
		Flooded and chilled; embryo killed	1
		Died during hatching	1
		Disappeared at hatching time; not known if hatched or not	16
Eggs hatched	103	Lost at ages 0-20 days	21
		Lost at ages 21-40 days	15
		Lost at ages 41-60 days	2
		Lost at ages 61-80 days	4
		Lost at 80+ days	1
Young flying	60		

that competition for food with their older nest-mates was an occasional cause of death at this period (Part 1, p. 41); there was no evidence of starvation in the later stages. Three young were almost certainly killed by crabs, the corpses of two of them being found on ledges near by, partly eaten. (Large crabs had been seen frequenting this and other nests, and no other potential predators could be found. When the holes in which the crabs lurked were blocked up, no other deaths of this kind occurred). Four young fell from their nests when part of the structure collapsed. In addition one fell from an intact nest and it is almost certain that others did. There was no evidence of predation of the young by man during the period of the study.

Food: General Remarks

There have been no detailed studies of the Oilbird's food. Most authors have stated that they feed mainly on the fruits of palm trees, while some have remarked that the family Lauraceae is also important. McAtee (1922) lists some seeds found in a Trinidad colony and refers to earlier accounts, pointing out that these may be of doubtful value owing to uncertainty of identification. For Venezuela, Pietri (1957) lists several species of palms, two species of Lauraceae and one of Burseraceae, and says that probably other kinds of fruit are eaten.

The feeding habits have been described in Part 1, pp. 31-32. Here it may be recalled that the birds pluck fruit in flight, at night, swallowing them whole. Nearly all the fruits taken have a firm pericarp enclosing a single rather large seed. Only the pericarp is digested, the seeds being later regurgitated intact.

In the course of the present study, regurgitated seeds were collected regularly at the Arima gorge colony from April, 1957, to September, 1961, samples of several hundreds, sometimes several thousands, being taken in each month. Most were collected from catching trays slung on the slopes below the nests, and others from the nests themselves. Care was taken to collect only freshly regurgitated seeds. Altogether, over 112,000 seeds were collected and examined. Samples were also collected from other caves as opportunity arose.

The identification of seeds in an area of rich tropical forest presents some difficulty. A few kinds, especially the distinctive seeds of some common palm species, were soon identified. Others remained unidentified for a long time, but in nearly every case the tree was eventually found in the forest. Two species were identified from herbarium material on the basis of whole

fruits and seeds collected in the cave. In the end only one important food tree remained unidentified. For the study of Oilbirds' food it is unfortunate that the Lauraceae is taxonomically a difficult family. There are many species with rather slight differences between them, and even in the important national collections there is a shortage of good material with mature fruits.

An incidental outcome of this study was the discovery of some species of Lauraceae new to Trinidad. *Beilschmiedia sulcata* represents a genus and species new to the island; *Licaria guianensis* and *Ocotea caracasana* were previously unrecorded from Trinidad; and specimens of an undescribed species, since named *Ocotea trinidadensis* Kostermans, were collected in the course of examining Lauraceae in the forest, though its fruit was not recorded in the Oilbird's food.

Composition of the Food

Table VI gives the totals of all the seeds collected from the Arima gorge colony throughout the period of the study. Eighteen species were important (over 100 seeds collected): 7 palms, 8 species of Lauraceae, 2 species of Burseraceae, and one species of Araliaceae[5]. Numerically, the Burseraceae outnumbered the Lauraceae in spite of the small number of species. Text-fig. 3 gives outline drawings of the more important seeds, with descriptive notes, and six kinds are illustrated in Plates I-III.

Most of the fruits eaten were regularly seasonal. This was especially true of the Lauraceae, which with only one exception showed clearly defined fruiting seasons varying little from year to year.

Palms.—The two important palms *Euterpe langloisii* and *Jessenia oligocarpa* were the two striking exceptions to the general rule that the food trees are seasonal in their fruiting. Seeds of *Euterpe* were present in every sample, and in many samples they outnumbered all other seeds (Table VIIa). *Jessenia,* a much larger fruit, was always present in much smaller numbers, and there was one long period, from November, 1959, to July, 1960, when it was very scarce and failed entirely for three months (Table VIIb). During this period, no trees in the forest could be found with ripe fruit.

In these two palms, each tree bears inflorescences and bunches of fruit in various stages of growth, and field observations showed that the fruit ripens very slowly. In addition, the ripe fruit has a hard and dry pericarp and probably

---

[5]Wrongly described in Part 1, p. 42, as probably myrtaceous.

remains in an edible condition on the tree for many weeks. Thus these two palms normally produce a rather constant supply of ripe fruit throughout the year. The cause of the general failure of *Jessenia* in 1959-1960 was not discovered; probably unsuitable weather some time previously had led to a gap in its flowering.

Euterpe is abundant in the forests of the Arima Valley, but *Jessenia* is rare, having its center of abundance in more low-lying swampy forests five or ten miles to the southeast. This is probably the main reason why the seeds of *Jessenia* were always less numerous than those of *Euterpe*.

Bactris cuesa, a small forest palm of the under-story, is much more seasonal in its fruiting than *Euterpe* and *Jessenia* (Table VIIc). Its season was even more sharply defined than is suggested by the table, as most of the fruits collected in the samples before May were unripe and regurgitated intact.

Roystonea, which was collected regularly in small numbers in the samples, does not grow in the Arima Valley. Its natural habitat in Trinidad is the low-lying swampy forest near the east coast, especially the Nariva Swamp, but it has been much planted in gardens and parks and the Arima gorge birds probably obtained its fruit from the town of Arima, five miles away. Table VIId shows that it was found in the samples in all months of the year.

Livistona chinensis is an introduced palm. It probably does not grow nearer to the cave than Arima, where it has been planted in small numbers. October to April are the main months for ripe fruit. Seeds of *Livistona* were found in moderate numbers in the samples from 1957 to April, 1959, but not thereafter. Probably this reflects a temporary habit of a few birds, or possibly the individuals visiting the *Livistona* trees were among those killed in the raid on the cave in September, 1959; the trees fruited abundantly in Arima in the two subsequent years.

Geonoma vaga is a small palm of the forest undergrowth, growing to about 12 feet. Its fruits are very small (about 4 mm. in diameter), the hard seed being covered by a thin pericarp. Like *Livistona*, it too was found in the samples only up to 1959, in the months January-July. It is remarkable that Oilbirds should be able to take its fruit at all, as it grows chiefly along streams and gullies, in rather dark parts of the forests, and surprising that they should have found it worth while to do so. Possibly one or two trees growing near the cave mouth were occasionally visited by the birds as they entered or left the gorge.

Unripe fruits of species of *Bactris* type were found in the samples somewhat irregularly but in all months of the year, occasionally amounting to an important fraction of the total food. The fruits were small and soft, without a seed, and many were regurgitated whole or only slightly broken up. Identification of most of them was uncertain, but probably the great majority were immature fruits of *Bactris gasipaes* (locally known as Pewa), a palm that is cultivated in small numbers for its edible fruits. In addition to the mature fruits, which contain a

TABLE VI. TOTAL NUMBERS OF FRUITS REPRESENTED IN COLLECTIONS FROM THE ARIMA GORGE COLONY, 1957-1961

PALMAE	*Euterpe langloisii*	45,520
	Bactris cuesa	6,315
	Jessenia oligocarpa	4,669
	Unripe *Bactris* sp.	663
	Livistona chinensis	489
	Roystonea oleracea	327
	Geonoma vaga	165
	Bactris sp.	17
	Desmoncus sp.	6
	Aiphanes sp.	3
	Bactris sp.	2
	Total	58,176
LAURACEAE	*Ocotea wachenheimii*	9,880
	Cinnamomum elongatum	5,831
	Ocotea caracasana	3,853
	Nectandra martinicensis	2,846
	Ocotea oblonga	2,370
	Nectandra kaburiensis	290
	Aniba firmula	267
	Nectandra membranacea	149
	Aniba trinitatis	70
	Aiouea schomburgkii	68
	Licaria guianensis	12
	Nectandra sp.	4
	Beilschmiedia sulcata	3
	sp. indet.	2
	Ocotea canaliculata	1
	Total	25,646
BURSERACEAE	*Dacryodes* sp.	21,895
	Trattinickia rhoifolia	6,731
	Protium sp.	1
	Total	28,627
ARALIACEAE	sp. indet.	148
OLEACEAE	*Linociera caribaea*	50
MYRISTICACEAE	*Virola surinamensis*	10
ANACARDIACEAE	*Tapirira guianensis*	7
SAPOTACEAE	*Pouteria minutiflora*	3
BORAGINACEAE	*Cordia bicolor*	1
MALPIGHIACEAE	*Byrsonima spicata*	1
UNIDENTIFIED	Several species	48
	Total	268
	Grand Total	112,717
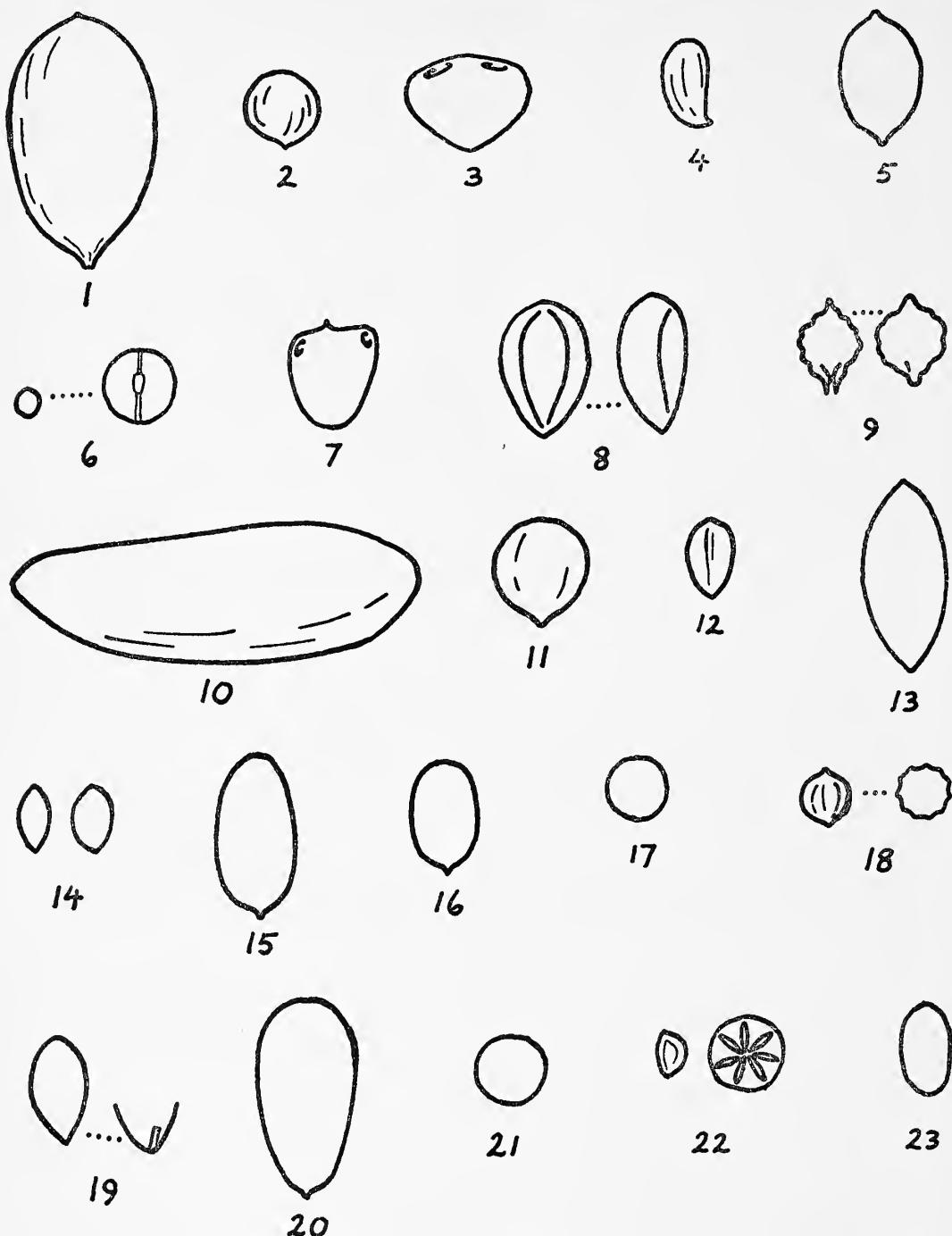
TEXT-FIG. 3. Seeds of the chief fruits eaten by Trinidad Oilbirds. (All natural size except where indicated.)

1. *Jessenia oligocarpa* (palm). Hard and fibrous, streaked dark and pale brown (see also Plate I).

2. *Euterpe langloisii* (palm). Hard and fibrous, pale yellow-brown. When dry, fibers curl off giving a hairy appearance (see also Plate I).

3. *Bactris cuesa* (palm). Hard and blackish, sometimes with pale fibers adhering; three pits (germ-pores) on the flattened end.

4. *Roystonea oleracea* (palm). Distinctively boat-shaped; pale fibrous surface, the fibers not coming away.

5. *Livistona chinensis* (palm). Smooth, hard, whitish, non-fibrous surface, with slight points at both ends, and slightly ridged down opposite sides (see also Plate II).

6. *Geonoma vaga* (palm). Hard and smooth; dark brown, with a pale apical spot and a pale longitudinal streak all the way round. (Left, natural size; right, enlarged.)

7. Unidentified *Bactris* sp. (palm). Hard and blackish, with three germ-pores, two with ridges above.

8. *Dacryodes* sp. (Burseraceae). Whitish, soon becoming stained, with demarcated "panel" becoming detached when the seed dries. When fruit is mature, seed contains seedling coiled up within.

9. *Trattinickia rhoifolia* (Burseraceae). Hard, brown; with two points at one end and one at the other, and complex ridges and depressions (see also Plate II).

10. *Beilschmiedia sulcata* (Lauraceae). Smoothish, pale brown; rather variable in shape and size, but typically very slightly curved. Soon splits into two halves (and germinates readily).

11. *Ocotea wachenheimii* (Lauraceae). Smooth, very slightly ridged; pale brown when fresh (see also Plate III).

12. *Ocotea oblonga* (Lauraceae). Dark brown, pitted with pale longitudinal streaks; fairly prominently ridged down opposite sides.

13. *Ocotea caracasana* (Lauraceae). Smooth, brown; regularly spindle-shaped.

14. *Cinnamomum elongatum* (Lauraceae). Smooth, pale to dark brown depending on maturity; somewhat variable in shape (two extremes shown); rather soft.

15. *Aniba firmula* (Lauraceae). Smooth, brown with blackish streaks; variable in size and shape, but with point at one end and rounded at the other, and usually broadest at pointed end (see also Plate III).

16. *Aniba trinitatis* (Lauraceae). Smooth, pale brown, unstreaked or faintly streaked; variable in shape, but characteristically widest near pointed end and often with slight ridges on opposite sides.

17. *Nectandra kaburiensis* (Lauraceae). Smooth, pale brown when fresh, nearly spherical; thin-skinned, with pinkish-purple endocarp.

18. *Nectandra membranacea* (Lauraceae). Brown, with slight points at both ends, and regular "fluting," as shown in transverse section.

19. *Nectandra martinicensis* (Lauraceae). Smoky brown, with black showing through in irregular longitudinal streaks. Slightly asymmetrical, one side more curved than the other, and apex with lip-like hilum (right, enlarged).

20. *Licaria guianensis* (Lauraceae). Smooth, dark brown, with point at narrow end; slightly ridged longitudinally; variable in size.

21. *Aiouea schomburgkii* (Lauraceae). Smooth, brown, mottled with dark markings; almost spherical.

22. *Araliaceae* sp. Seeds flattish, roughly half-moon shaped; embedded radially in berry as shown.

23. *Linociera caribaea* (Oleaceae). Pale brown, with a network of raised veining; bluntly oval.

large seed and are probably too large for Oilbirds to swallow, they produce small fruits that do not develop to maturity. One owner of a small estate told me that he had shot an Oilbird that was visiting his Pewa trees.

Besides these seven main kinds, there was a very small number of palm seeds of other species. Several seeds were close to *Bactris cuesa* but differed consistently in shape and probably represented other species. The taxonomy of this section of the genus is difficult, and there has been some fine splitting of species (Bailey, 1947). *Aiphanes* sp., ? *minima*, of which three seeds were found, is a cultivated species with edible fruits (locally known as "edible gri-gri"). Six seeds were referred to *Desmoncus*, a genus of spiny climbing palms, but they were not the common species *D. major*.

Lauraceae.—Table VIII shows the percentage

occurrence of the ten most important species of Lauraceae in the food. With one exception (*Ocotea wachenheimii*), they all had well-defined fruiting seasons which were much the same in all years; in all but two of them the season fell mainly in the months March-June. One of the exceptions, *Aniba firmula*, fruited rather earlier, in December-April, while the other, *Nectandra martinicensis*, was the only species with a fruiting season at the end of the year, from September to November. Table X summarizes the fruiting seasons of these ten regularly occurring species, and shows clearly the importance of the March-June peak.

In number of seeds found in the samples, *Ocotea wachenheimii* was the most important species, and, as mentioned above, it was the only species with an irregular fruit season. In all years a main fruit season began in November

TABLE VII. SEASONAL OCCURRENCE OF PALMS IN THE FOOD SAMPLES

		Percentage of the total in the different months											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
(a)	1957	. . . . . .	. . . . . .	. . . . . .	20	28	51	64	74	58	43	75	64
Euterpe	1958	26	33	31	28	31	18	16	37	46	53	45	4
langloisii	1959	9	44	54	49	26	28	6	2	36	32	41	82
	1960	40	15	37	58	52	21	15	16	30	54	78	86
	1961	62	54	73	56	45	44	30	6	21	. . . . . .	. . . . . .	. . . . . .
(b)	1957	. . . . . .	. . . . . .	. . . . . .	17	7	3	7	8	12	13	15	10
Jessenia	1958	5	6	2	1	1	2	4	11	12	7	8	2
oligocarpa	1959	6	14	25	20	5	3	3	1	2	1	+	+
	1960				+	+	+	+	1	9	12	11	9
	1961	3	1	1	1	2	6	5	2	3	. . . . . .	. . . . . .	. . . . . .
(c)	1957	. . . . . .	. . . . . .	. . . . . .		1	4	9	10	11	3	1	+
Bactris	1958	+	+	+	+	1	3	17	33	18	15	25	2
cuesa	1959			1	+	4	17	55	74	17	10		+
	1960	+		+	+	2	5	4	7	11	1		
	1961			+	+	+	5	23	29	16	. . . . . .	. . . . . .	. . . . . .
(d)	1957	. . . . . .	. . . . . .	. . . . . .		+	+	+	1	1	1	2	+
Roystonea	1958	+	+	+	+	1	1	+	+	+	+		
oleracea	1959			+		+				+		+	+
	1960		+	+	1	2	+				+		
	1961		+	+					+		. . . . . .	. . . . . .	. . . . . .

Note (applying also to Tables VIII and IX): +, less than one percent. Dots (. . . .), no sample collected. Where the year is omitted, no seeds were found in that year.

or December, which lasted from four to six months. In 1958 and 1960, and less markedly in 1961, there was a secondary minor fruit season in June or July. The fruiting period April-July, 1957, might have been either the tail-end of a long and prolific fruiting beginning at the end of the previous year, or it might have been a combination of such a fruiting with a secondary fruiting in June-July.

A single tree of *O. wachenheimii,* growing near the cave, was kept under observation from January, 1958, to September, 1961. It had ripe fruit regularly from late November or December to February, and had none in June or July. Another tree on an exposed ridge at a higher altitude, which was visited less regularly, had nearly ripe fruit in June in two years. Three out of the four samples of seeds taken from caves at the extreme western end of Trinidad in July and August had good numbers of seeds of *O. wachenheimii,* including one collected in 1959 when none were being taken by the birds in the Arima gorge. It seems probable that individual trees of this species have one main fruiting season per year, which may be either November-February or June-July, and it may be that the June-July fruiting season is more general in the drier parts of the island.

Beilschmiedia sulcata is not included in the ten main species of Lauraceae, as only three seeds were found in the Arima gorge (in March, May and June), but it is one of the most important fruits taken by the Oilbirds in the caves to the east of the Arima Valley. Fresh seeds were found in nearly every month of the year in these caves, but their presence was irregular. Thus there were good numbers in May and December, 1957, but none in December, 1959, or May, 1960. *Beilschmiedia* grows at high altitudes on the Aripo massif, where the rainfall is extremely high and probably less seasonal in its distribution than at lower altitudes, and the fruiting of trees may be less regularly seasonal.

Burseraceae.—The most important species, *Dacryodes* sp., fruited in alternate years during the period under study (1958, 1960 and 1962), very small numbers of seeds being found in the intervening years. It is a common tree above 1,500 feet in the Northern Range and when it was in fruit its seeds often outnumbered everything else in the samples. Individual trees remain in fruit for many weeks, as the fruits, borne in large bunches, ripen slowly and irregularly. In the intervening years, some trees that were examined produced fruit which grew to full size and looked normal but were in fact hollow. There was no evidence that these were taken by Oilbirds.

TABLE VIII. SEASONAL OCCURRENCE OF LAURACEAE IN THE FOOD SAMPLES

		Percentage of the total in the different months											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ocotea	1957	....			28	28	20	11	2	+	+		
caracasana	1958		+	3	1	1							
	1959		+	1	3	2	+						
	1960		+	2	1	+							
	1961		1	4	4	4	2				....		
Ocotea	1958			3	13	1		+					
oblonga	1959				21	17	1						
	1960				3	2							
	1961				3	7	4				....		
Ocotea	1957	....			7	7	3	1	+				23
wachen-	1958	65	39	1				7	11	1		12	90
heimii	1959	56	1										1
	1960	42	28	3	+		1	1	+			1	2
	1961	34	44	21	4	+		+			....		
Cinna-	1957	....			16	18	10	+					
momum	1958					3	14	5					
elongatum	1959				3	41	15						
	1960			+	+	1	1						
	1961		+		27	37	9				....		
Nectandra	1957	....							1	11	28	1	
martini-	1958									20	19	3	
censis	1959									26	50	56	2
	1960	+	+							11	22	5	
	1961								+	+	....		
Nectandra	1959				+	1							
mem-	1961				3	1					....		
branacea													
Nectandra	1957	....				1	1	+					
kaburiensis	1958					1	1	+					
	1959					+	1						
	1960					+							
	1961					2	1				....		
Aniba	1958	2	+										
firmula	1959												+
	1960	+	3	4	+								
Aniba	1958			+	+								
trinitatis	1960		+	1	+								
	1961			+	1	+					....		
Aiouea	1958			1	1	1	2						
schom-	1961				+						....		
burgkii													

NOTE: The following species never accounted for as much as 1% of the monthly sample: *Licaria guianensis* (found in May, 1958, and March-May, 1961); *Beilschmiedia sulcata* (found in March, May and June in three different years).

Trattinickia seeds were found in the food samples in nearly every month, but comprised an important fraction of the total only in the months June-September. A single tree kept under observation for over 2½ years fruited in 1959 and 1961, but not in 1960. After the first lot of fruit was gone most of the leaves fell and new flowers appeared seven months after the growth of the new leaves; the fruits then took ten months to ripen. The complete cycle took two years. Three other trees that were less regularly observed fruited at the same time as this

TABLE IX. SEASONAL OCCURRENCE OF BURSERACEAE AND ARALIACEAE IN THE FOOD SAMPLES

		Percentage of the total monthly sample											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Dacryodes	1957	. . . .					+	+					
sp.	1958	+	18	57	56	62	60	47	5	+	1		
	1959				+								3
	1960	12	53	54	37	39	71	68	35	+			
	1961								+		. . . .		
Trattinickia	1957	. . . .			4	7	6	6	4	5	6	3	1
rhoifolia	1958	1	2	1	1	1	1	2	1	1	4	4	1
	1959	5	3	1	2	6	34	36	23	17	6	1	6
	1960	4	1	+	+	+	+	11	41	37	4	1	+
	1961	+	+	+		1	28	42	59	47	. . . .		
Araliaceae	1957	. . . .							+	1	+	+	
sp.	1958								+	+	+	1	+
	1959								+	2	1		
	1960						+		+	2	+		
	1961									2	7	. . . .	

tree. But the continuous presence of *Trattinickia* seeds in the samples shows that other trees must have fruited in the intervening years. Like *Dacryodes*, *Trattinickia* trees remain in fruit for several weeks.

Araliaceae.—The only regularly eaten fruit that did not conform to the usual type (firm pericarp surrounding a single seed) remained unidentified. The tree was never found, and since the seeds were not found in any cave except the Arima gorge, though five samples were collected at other colonies at times when the seeds were regular in the Arima gorge samples, it is hard to avoid the conclusion that either the tree is very local or its exploitation is an idiosyncrasy of the Arima gorge birds. Occasional regurgitation of whole fruits enabled the family to be determined with reasonable certainty (see also Appendix).

Other Species.—*Byrsonima spicata*, *Virola surinamensis*, *Pouteria minutiflora*, *Tapirira guianensis* and *Cordia bicolor* are all common trees in the Arima Valley, and their fruits are much eaten by other kinds of birds. Their great rarity in the food samples indicates that Oilbirds in general avoid them. *Byrsonima*, *Cordia* and *Pouteria* all have more or less succulent, acid fruits, while *Virola*, the wild nutmeg, has a net-like aril enclosing the seed. All these are very unlike the sort of fruit usually eaten by Oilbirds. *Tapirira*, also a common tree, has a fruit that is superficially like that of *Dacryodes* and is much eaten by pigeons. The reason for its avoidance by Oilbirds is discussed in a later section (p. 217).

Only one tree of *Linociera caribaea* (Oleaceae) was found in the Arima Valley, and two others in a valley a few miles to the east. Thus

TABLE X. FRUITING SEASONS OF THE TEN MOST IMPORTANT SPECIES OF LAURACEAE

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Aiouea schomburgkii			×	×	×	×						
Aniba firmula	×	×	×									
Aniba trinitatis			×	×								
Cinnamomum elongatum				×	×	×	×					
Nectandra martinicensis									×	×	×	
Nectandra membranacea				×	×							
Nectandra kaburiensis					×	×						
Ocotea caracasana			×	×	×	×						
Ocotea oblonga				×	×	×						
Ocotea wachenheimii	×	×	×	×	×	×	×	×			×	×
Number in fruit in each month	2	2	5	7	7	6	2	1	1	1	2	1

it is not a common tree, and the presence of its seeds, in moderate numbers, in the food samples in one year only may indicate that a few birds found a tree but did not revisit it in subsequent years.

There was evidence of only one kind of fruit being eaten besides those found in the food samples. A reliable observer reported an Oilbird feeding on unripe fruits of the Tonka Bean (*Dipteryx odorata*) in an Arima garden. The mature fruit, about three or four inches long, is far too large to be taken. It is perhaps significant that the Tonka Bean has a pervasive scent.

THE FOOD AT OTHER COLONIES

Each time one of the other Trinidad colonies was visited, a food sample was collected from below the nests, and sometimes from the nest themselves when they were accessible. On each occasion, hundreds of seeds were examined and an attempt was made to collect a sample showing the proportions in which the different kinds were present. Care was taken to collect only fresh seeds. Altogether, 18 samples were collected.

In general, the main kinds of fruit were the same as were being eaten by the birds at the Arima gorge colony in the same period, and they were in roughly the same proportions. Not a single seed was found at these other colonies that was not at some time found at the Arima gorge colony. Thus there is little doubt that the food of the Arima colony is typical of the Trinidad population as a whole. There were, however, some differences between the samples from these various colonies, which may be briefly summarized.

Oropouche Cave. — The most easterly cave, situated in an area of high rainfall, but at a low altitude. Eight samples were collected in seven different months. The composition was much the same as at the Arima colony, but *Beilschmiedia* was regular, sometimes in large numbers, and *Trattinickia* was never found. Two samples contained a smaller variety than was found at the Arima colony at the same time, the other six approximately the same variety.

Aripo Caves.—These are the highest caves, in montane forest. Six samples were collected in four different months. The composition was much the same as the Oropouche cave (again, *Trattinickia* was never found), but the variety was regularly less than at the Arima colony. For example in December, 1957, only *Jessenia* and *Beilschmiedia* could be found, although eight kinds of fruit were being taken at the Arima

colony. The reason may lie partly in the poorer floristic composition of the montane forest (Beard, 1946).

La Vache Cave.—Two samples, both in August. The composition and variety was almost exactly the same as at the Arima colony at the same time.

Huevos Cave.— Two samples, in July and August. The composition was similar to that at the Arima colony, but *Ocotea caracasana* was abundant in the August sample (not present at the Arima colony; Table VIII), and *Livistona* was present in both samples. The latter was almost certainly obtained from Port-of-Spain gardens and parks.

It is noteworthy that *Trattinickia,* which was taken regularly by the Arima birds, was also present in three of the four La Vache and Huevos samples, but was never found in the samples from the Oropouche and Aripo caves. This strongly suggests that the tree is rare or absent east of the Arima Valley.

THE FORAGING RANGE

Extravagant claims have been made for the distances travelled by foraging Oilbirds in Venezuela (*e.g.,* 80 leagues—Funck, 1844), but without convincing evidence. For Trinidad the evidence, incomplete though it is, suggests that they can and do fly to places 15, or occasionally even 30 miles distant from the cave in search of food, but that foraging distances are usually much shorter.

Oilbirds have several times been seen feeding on the palm trees round the Queen's Park Savanna in Port-of-Spain, 14 miles from the Huevos cave and 8 miles from La Vache cave. The presence of numerous *Livistona* seeds in the Huevos samples, but not in the La Vache samples, suggests that the Huevos birds are involved. The La Vache birds would in any case have to cross hills of 1500 feet or more to reach Port-of-Spain, while the Huevos birds need not rise much above sea level. This is the longest foraging distance for which there is direct evidence, but almost certainly the Huevos birds at times fly farther afield. The forests within five miles of the Huevos cave are of dry monsoon type, far poorer than those to the east; so that the birds may often have to fly several miles to suitable feeding grounds. *Jessenia,* which was present in the Huevos samples, probably does not grow within 15 miles, and *Beilschmiedia,* of which one seed was found, has so far been found only on the Aripo massif, 30 miles to the east. Hence the Huevos birds must often fly considerable distances to feed, and they must

be at an ecological disadvantage compared with the birds in the caves further east. It is not known whether they visit Venezuela, of which the nearest point is only nine miles away to the west.

The Arima gorge birds visit Arima, five miles away, where they take *Livistona* fruits, and probably regularly visit the swampy forests between Arima and Valencia, eight or nine miles away, since *Jessenia* is not commonly found nearer than this. But they cannot regularly visit the montane forest of the Aripo massif, only five or six miles away to the east, since in over 112,000 seeds there were only three of *Beilschmiedia*, which forms an important part of the food of the birds of the Oropouche and Aripo caves. Conversely, *Trattinickia* was an important element in the food of the Arima gorge birds, but was never found in the samples from Oropouche and Aripo, showing that the birds from these caves do not normally visit the drier forests only a few miles to the west.

AVAILABILITY OF FOOD

If a fruit-eating bird is found to be taking a greater variety of fruits at some seasons than others, it could mean that highly acceptable food of several kinds is more abundant at that season than at others, or it could mean that its preferred food is scarce and it is having to seek other kinds. Conversely, few kinds of fruit in the diet might mean either that food is scarce, or that it is abundant and the bird is concentrating on the kinds that it most prefers. A bare analysis of food items in the diet may not enable one to decide between these two opposite possibilities. However, for the Oilbird we may safely conclude that when it is taking a large number

of different kinds of fruit its food is especially abundant. The different fruits which they take and which make up the normal variety (the exceptional ones being left out of account) all recur regularly in their diet year after year, so cannot be regarded as foods to which they turn in times of shortage. Further, observations showed that they were taking the fruits as they became available in the forest, the periods when they were found in the food samples corresponding closely to the periods when the trees were observed to have ripe fruits. This again suggests a regular and normal exploitation of a seasonally varying food supply.

On this criterion of available variety, the Oilbird's food supply shows well-defined seasonal changes in abundance (Text-fig. 4). The greatest variety of food is available in the months April-June. It has already been shown that the breeding season is very long, and young birds may be in the nest in any month of the year. But there is a marked peak of laying in the months December-May, which results in more young birds being in the nests in the months March-June than at any other time (Text-fig. 4). This suggests that the breeding season is timed so that most young are in the nest when food is most abundant, though with such a long breeding season and extremely long nestling periods the adjustment cannot be very exact.

For the Venezuelan population, living in a more seasonal environment with a more marked dry season, the seasonal availability of food may show more marked fluctuations than in Trinidad, and the adaptation of breeding season to the fluctuating food supply may be more important. But precise data from Venezuela are
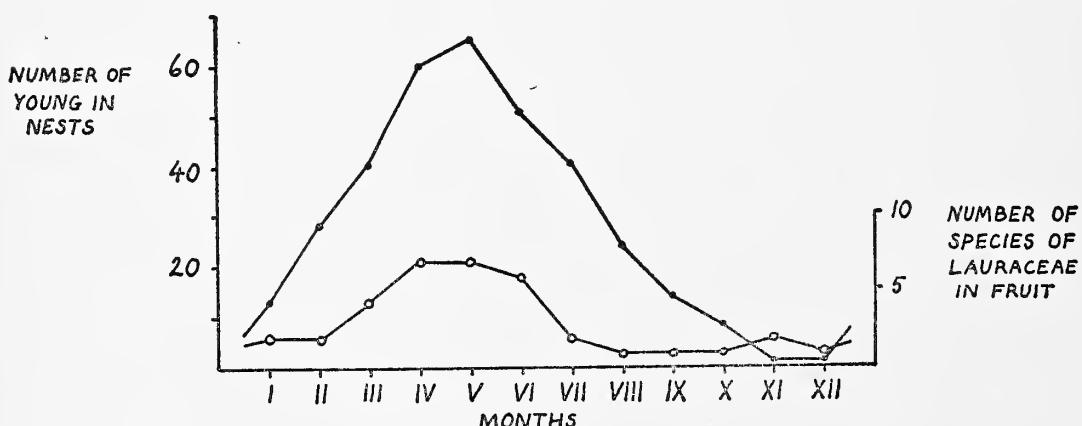
TEXT-FIG. 4. Relationship between number of young in the nests in each year, all years combined (dots), and number of species of Lauraceae in fruit in each month (open circles).

lacking, both on the Oilbirds' breeding season and on the fruiting seasons of the food trees.

Regurgitation of Whole Fruits

As already mentioned in Part 1, the seed samples regularly contained a proportion of whole fruits which had been regurgitated intact, and others from which only part of the pericarp had been removed. A few of these were unripe fruits that had been picked by mistake, or in apparent anticipation of the time when they would be ripe (especially *Bactris cuesa* in March and April), but many were ripe and there was no obvious reason why they should not have been digested. In some months 10% or more of all fruits were intact but usually the proportion was between 1 and 5%. The percentage regurgitated whole showed no correlation with the availability of food, as measured by the number of food trees that had ripe fruit in that month, but was related to the state of breeding in the colony. In each year, the highest percentages of whole fruits were found towards the end of the main period when young were in the nests (July-September in 1958, April-May in 1960 and June-July in 1961). In 1959, when very few young were reared, the percentage of undigested fruits never rose above 3%.

The way in which the pericarps are digested and the seeds regurgitated is not properly understood. Young birds taken from the nest and kept under observation would regurgitate clean seeds and unaltered whole fruits in the same batch; no seeds were regurgitated with the pericarp in a half-digested or softened state, but some were regurgitated with it partially stripped off. The few stomach contents examined also showed a mixture of whole fruits and stripped seeds. Thus one must conclude that no digestion takes place in the stomach, but that the pericarps are gradually stripped off by the muscular action in the stomach and passed backward into the intestine, where digestion takes place. Once the pericarp has begun to come away from a seed, it will usually soon be stripped off, while another fruit eaten at the same time may still be intact.

Probably regurgitation begins to take place a certain length of time after the food has been eaten, and is largely under involuntary control except when an adult is feeding its young (Part 1, p. 42). By the time it begins to take place, most fruits will have been stripped of their pericarps, but a few may have remained intact; hence the regular occurrence of small numbers of whole fruits in the food samples at all seasons.

Nestlings taken out of the nest, and kept all day before being returned to the nest in the evening, regurgitated a high proportion of whole fruits: 118 (28%) of the total of 428. Regurgitation may perhaps have been abnormal, owing to the disturbance of being removed from the nest, but it seems likely that at any rate the larger nestlings, which receive very ample feeds, may normally regurgitate a rather high proportion of intact fruits. In addition the feeding process itself involves much strenuous activity by both adult and nestling (Part 1, p. 41), and some fruits may be dropped as the food is passed from adult to young. It is thus not surprising that late in the nestling period a rather large number of whole fruits are found on the nests and the slopes below the nests. From the ecological viewpoint, it suggests an ample food supply, since if the supply of food were often critical it is unlikely that such wasteful behavior could persist.

Food Value of the Fruits Eaten, and Its Ecological Implications

Oilbirds range widely over the forest at night, and of the many fruits that are available they take only a few kinds, avoiding many others that are eaten by diurnal fruit-eating birds. Almost without exception, as already mentioned, the fruits which they regularly take are kinds that have a firm, in some cases hard, non-succulent pericarp, enclosing a single seed. From this it seems probable that succulent fruits have insufficient food value for their weight to be an economical food for Oilbirds, which not only feed on the wing but must fly considerable distances to their food trees.

To test the point further, the food values of some of the more important kinds of fruit eaten by Oilbirds were determined, through the courtesy of Professor J. K. Loosli of the New York State College of Agriculture. They are given in Table XI, which also lists for comparison the equivalent values for some common succulent fruits eaten by birds and men. It will be seen that the fruits taken by Oilbirds have an extremely high fat content and on average a markedly higher protein content than the succulent fruits; the fat:protein ratio is in fact much like that of a nut kernel. (In fat content they are exceeded by two well-known fruits, the avocado pear (59%) and the olive (68%), but the fat content of these may well have been increased by artificial selection. They belong to families which are represented in the Oilbird's diet, the Lauraceae and Oleaceae).

The food value of the fruits taken by Oilbirds in comparison with succulent fruits is even

TABLE XI. ANALYSIS OF DRIED PERICARPS OF FRUITS EATEN BY OILBIRDS,
AND SOME OTHER FRUITS

		Percentage composition		
		Protein	Fat	Carbohydrates, ash and crude fiber
Fruits regular in Oilbird's diet	LAURACEAE *Cinnamomum elongatum*	9	44	47
	Ocotea oblonga	11	19	70
	Ocotea wachenheimii	14	34	52
	BURSERACEAE *Dacryodes* sp.	11	24	65
	PALMAE *Bactris cuesa*	13	39	48
	Jessenia oligocarpa	5	26	69
Fruits occasionally taken but generally avoided	LAURACEAE *Ocotea canaliculata*	8	34	58
	ANACARDIACEAE *Tapirira guianensis*	5	7	88
Some succulent fruits	Apple	2	Tr.	98
	Fig	5	Tr.	95
	Gooseberry	4	Tr.	96
	Grape	4	Tr.	96
	Red currant	6	Tr.	94

NOTE: Data for the first seven supplied by Professor J. K. Loosli, Cornell University, *in litt.*; percentages for *Tapirira* by Mr. J. S. Leahy, Huntingdon Research Centre, England (*in litt.*); percentages for last five reworked from data given in McCance & Widdowson (1946).

greater than is suggested by this table, as their water content is lower. In most succulent fruits the water content of the pericarp is between 75 and 85%, while that of the palms eaten by Oilbirds is probably less than 50% (exact figures not available), that of *Dacryodes* 60%, and that of *Ocotea wachenheimii* about 75%. Thus there seems little doubt that Oilbirds select the kinds of fruit that they do primarily because their food value is, for fruits, unusually high.

It may be noted that, although the palm fruits have drier pericarps than the Lauraceae, their seeds are relatively larger, weighing 54-69% of the total weight of the fruit in the three most important species, as against 33-42% in the three species of Lauraceae for which there are data (Table XII). Thus weight for weight they yield approximately the same amount of nutritive matter.

It was mentioned in Part 1 that many of the trees on which Oilbirds feed are spicy or aromatic, and it was suggested that the olfactory sense may be important in enabling them to locate the food trees (see also Bang, 1960, for anatomical evidence supporting this suggestion). The situation in the Arima Valley in March-May, 1961, was particularly illuminating in this respect. Three common species of Lauraceae were in fruit at the same time, *Cinnamomum elongatum, Ocotea oblonga* and *O. canaliculata*. The first two had fruited regularly in previous years (Table VIII), but *O. canaliculata* had not been observed in fruit in the lower part of the Arima Valley, and certainly cannot have fruited prolifically. (Higher in the valley, one tree under observation had produced a little fruit in 1958 and 1959). The Oilbirds, as usual, took large quantities of *Cinnamomum* and *O. oblonga* fruit, but only one seed of *O. canaliculata* was found among the thousands examined. Samples of dried pericarp of all three were analyzed (Table XI). In fat content *O. canaliculata* was intermediate between the other two, being exactly the same as *O. wachenheimii*,

TABLE XII. WEIGHTS OF FRUITS EATEN BY OILBIRDS

	Number weighed	Mean weight (gm.)	Mean weight of pericarp (gm.)
LAURACEAE			
Cinnamomum elongatum	5	0.6	0.4
Ocotea caracasana	2	9.5	5.0
Ocotea wachenheimii	16	3.3	1.9
BURSERACEAE			
Dacryodes sp.	10	2.8	1.3
Trattinickia rhoifolia	2	1.5	1.0
PALMAE			
Bactris cuesa	10	4.1	1.9
Euterpe langloisii	20	1.3	0.4
Geonoma vaga	15	0.17	0.10
Jessenia oligocarpa	6	16.8	6.2
Livistona chinensis	8	2.0	0.9

which is much eaten. In protein content it was only 1% lower than *Cinnamomum. O. canaliculata* would thus seem from its nutritional value to be a perfectly suitable food for Oilbirds. There was, however, a striking difference between the three samples: the pericarp of *Cinnamomum* was highly aromatic, that of *O. oblonga* noticeably so, but that of *O. canaliculata* absolutely non-aromatic. These differences were noted without exception by several persons who where presented with the samples in random order and asked to comment on them.

A further comparison was made between the three "gommiers," *Dacryodes* and *Trattinickia* which are much eaten, and *Tapirira guianensis* which is avoided, though locally it is the commonest of the three. The local name reflects a general similarity between these trees, all of which produce gum from the bark, have rather similar compound leaves and bear bunches of fruit of much the same size and type. The Oilbirds' selection of the first two species and avoidance of the third may have the same cause as in the three Lauraceae: *Dacryodes* and *Trattinickia* are aromatic, but *Tapirira* is not. However, analysis of *Tapirira* fruits (Table XI) showed that their fat and protein content is markedly low compared with the fruits that are regularly eaten, so that it is probably not an economical fruit for Oilbirds to take.

The palms on which Oilbirds feed are not aromatic. It seems likely that they are located visually, a method which would be easier for palms, with their characteristic shape, than for dicotyledonous trees.

These facts strongly suggest that, while the food value of the fruit is of primary importance, **in** searching for suitable food trees other than palms Oilbirds are guided to an important degree by the olfactory sense. This is in the main an efficient method, since most of the trees on which they feed, in the families Lauraceae and Burseraceae, are aromatic; but it results in their missing some species which from the nutritional standpoint are suitable.

In Part 1, p. 42, it was shown that the three young Oilbirds which were investigated ate about one-quarter to one-third of their body-weight in the course of a night. Using these figures, and the known food values of the fruits eaten, we can make a rough assessment of the total amount of protein, fat and carbohydrate eaten by a nestling Oilbird in the course of its growth. We may consider only the first 70 days of its nestling period, when it is increasing in weight.

If we assume that it eats one-third of its weight every night (though this figure may well be a little too high for the last 20 days), and take an average growth-curve from 14 gm. at hatching to 600 gm. at 70 days (Part 1, Table III), we find that in the course of its first 70 days a nestling Oilbird will eat about 7,600 gm. of fruit. Using the mean figure for the Lauraceae (Table XII), this corresponds to 4,560 gm. of pericarp, and to 1,370 gm. of dried pericarp (using figures for *Ocotea wachenheimii*). Analysis of the percentage composition of dried pericarp showed that protein content was around 10% for most species, fat content about 30%, and carbohydrate content about 35%. Thus 1,370 gm. of dried pericarp will give about 137 gm. of protein, 410 gm. of fat, and 480 gm. of carbohydrate.

The total nitrogen in proteins is about 16% by weight. Thus 137 gm. will contain about 22

gm. of nitrogen. It is not possible to make more than a rough assessment of the total nitrogen in a 70-day nestling Oilbird, but the following figures may be used provisionally. Probably some 250 gm. of the total weight consists of fat, and the remaining 350 gm. represents the nitrogen-containing fraction, as the weight of the adult, which has little fat, is on average 415 gm. and the body dimensions, muscular development and feathering of the 70-day nestling are somewhat less than in the adult. No figures have been found for the total protein content of a bird, but using the figures for fresh meat (around 20%) and allowing a reduction for blood and bone, we may take 15% as a reasonable figure. Thus we may estimate that a 600 gm. nestling Oilbird will contain roughly 8.5 gm. of nitrogen (350 gm. × 15% × 16%). This figure agrees well with an independent estimate from data given by Rubner (quoted in Brody, 1945). According to Rubner, one kg. of normal body substance (*i.e.*, including all organs in due proportion) contains about 30 gm. of nitrogen. Consequently 350 gm. will contain about 10.5 gm.

In the absence of data on the nutritional value and amino-acid composition of the proteins in the nestling Oilbird's diet, we can do no more than guess whether an intake of 22 gm. of nitrogen would be adequate to produce 9 or 10 gm. of nitrogen in the body. But the efficiency of utilization of dietary nitrogen derived wholly from fruit pericarps, over a period of 70 days, could hardly be expected to exceed 50%, which suggests that the young Oilbird is growing as fast as is possible on such a diet.

Turning to the energy requirements of the growing Oilbird, we may make another rough calculation. The total intake of food, as estimated above, yields 6,343 calories (on the basis of 4.1 cal. per gm. of carbohydrate, 9.3 cal. per gm. of fat, 4.1 cal. per gm. of protein; Best & Taylor, 1949). The calorific value of a 70-day Oilbird weighing 600 gm. is not exactly known, but it may be estimated at 3,025 cal., on the basis of 9.3 cal. per gm. of fat and 2 cal. per gm. of the rest of body-substance. This gives a gross efficiency of growth, in respect of consumed metabolic energy, of about 48%. Brody (1945) quotes equivalent figures for rats and chickens: for rats, gross efficiencies up to 13.6%; for slow-growing chickens, gross efficiencies up to about 20%. The apparently very high gross efficiency of the nestling Oilbird is probably made possible by the development of the thick insulating layer of fat, the growth of a thick covering of down and relative inactivity.

These calculations, rough though they are, probably have enough validity to justify the conclusion that on a diet of pericarps of palm and lauraceous fruits young Oilbirds could not obtain enough nourishment to develop any faster than they do. Thus the very long nestling period may be regarded primarily as an adaptation to the very specialized diet, as provisionally suggested in Part 1, p. 44. This adaptation could not have been acquired unless the birds had available to them nest-sites safe from most natural predators.

This conclusion rests on the assumptions that the parents could not provide more food for the nestlings, or that if they could, the nestlings would not be able to deal with a greater quantity of bulky food per day. Neither of these assumptions can be tested on present evidence, but the facts that Oilbirds have often to fly several miles for food, that their flight-speed in level flight is not high, and that they spend up to four hours apparently feeding themselves before they return with food for the young (Part 1, p. 41), all suggest that the three or four feeds in the night that were recorded are as many as are normally possible under the circumstances.

The work was made possible by generous grants from the National Science Foundation (G 4385 and G 21007), for which grateful acknowledgement is made.

Summary

The present adult population of Oilbirds in Trinidad, in the eight known colonies, is estimated to be 1,460. Five small colonies have been exterminated in recent years. The population is considered to be in no immediate danger, but is potentially vulnerable.

The breeding season is very long, extending from December to September, but nearly all clutches are laid before June. The moult takes place mainly in June-November, but it lasts so long that in some individuals it almost certainly overlaps the beginning and/or end of the breeding cycle. There is evidence that birds may begin a second wing-moult before the first is complete.

Clutch-size varies from 1 to 4 eggs, the mean being 2.7. It was found to decrease in the course of the breeding season, probably in correlation with decreasing abundance of food.

Nearly 50% of observed nestings were successful, earlier nestings being more successful than later ones. The causes of failure were various; there was no evidence of starvation of nestlings except perhaps occasionally in the first few days.

An analysis is given of 112,000 seeds collected from the Arima gorge colony. The important fruits comprised 7 species of palms, 8 of Lauraceae, 2 of Burseraceae, and 1 of Araliaceae. Two important palms provided a more or less steady supply of food throughout the year: the Lauraceae were nearly all regularly seasonal. Evidence is given that Oilbirds may fly up to 30 miles for their food, but foraging distances are usually much shorter.

The greatest variety of food is available in the months April-June, corresponding to the period when most young are in the nest. In all months of the year, a proportion of the fruits are regurgitated whole, rising to 10% or more in the latter part of the breeding season.

The food values of some of the chief foods are analyzed, and it is concluded that on a diet of fruit pericarps young Oilbirds could not develop much faster than they do. The extremely long fledgling period is thus primarily an adaptation to the specialized diet.

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APPENDIX
Systematic List of the Oilbird's Food Trees

The order and nomenclature follow Beard (1946), with alterations and additions as noted.

Lauraceae

Aiouea schomburgkii Meissn.
Aniba firmula (Nees) Mez
 Aniba panurensis Mez, listed in Beard, is a synonym.
Aniba trinitatis (Meissn.) Mez
Beilschmiedia sulcata (R. & P.) Mez
 Genus and species new to Trinidad.
Licaria guianensis Aubl.
 New to Trinidad.
Nectandra martinicensis (Jacq.) Mez
Nectandra membranacea (Sw.) Griseb.
Nectandra kaburiensis Kosterm.
 Listed in Beard as *N. surinamensis* Mez.
Ocotea canaliculata (Rich.) Mez
Ocotea caracasana (Nees) Mez
 New to Trinidad.
Ocotea oblonga (Meissn.) Mez
Ocotea wachenheimii R. Benoist
 Ocotea arenaensis R. L. Brooks, listed in Beard, is a synonym.
Cinnamomum elongatum (Vahl) Kosterm.
 Listed as *Phoebe elongata* (Vahl) Nees in Beard. *Phoebe* is synonymous with *Cinnamomum,* fide Kostermans.

Myristicaceae

Virola surinamensis (Rol.) Warb.

Burseraceae

Dacryodes sp.
 Specific determination depends on specimens with flowers, which have not yet been obtained. Previously known from Trinidad on the basis of one old specimen, but locally well-known as "mountain incense" or "gommier montagne," and referred to under the latter name by Beard.

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Trattinickia rhoifolia Willd.

Malpighiaceae
Byrsonima spicata (Cav.) Rich.

Anacardiaceae
Tapirira guianensis Aubl.

Araliaceae

The atypical fruit which remained unidentified (p. 212) is referred to this family with reasonable certainty by Mr. N. Y. Sandwith (Kew) and Dr. A. C. Smith (U.S. National Museum), who were sent detailed drawings of the mature fruit. The latter suggests the genera *Dendropanax* or *Schefflera* as being the most likely.

Sapotaceae
Pouteria minutiflora (Britt.) Sandwith

Oleaceae
Linociera caribaea (Jacq.) Knobl.

Boraginaceae
Cordia bicolor DC.
 Cordia lockhartii Kuntze, listed in Beard, is a synonym.

Palmae
Bactris cuesa Crueg.
Euterpe langloisii Mart.
 No consistent differences could be found between the many *Euterpe* seeds and fruits in the food samples. All appeared to come from the common *Euterpe* of the forests of the Northern Range, for which the name *langloisii* may provisionally be used. The species have been very finely split (Bailey, 1947).
Geonoma vaga Griseb. & Wendl.
Jessenia oligoarpa Griseb. & Wendl.
Livistona chinensis R. Br.
Roystonea oleracea (Jacq.) Cook

EXPLANATION OF THE PLATES

PLATE I

FIG. 1. Seeds and whole fruit (upper right) of *Jessenia oligocarpa*. (Millimeter scale is shown in this and the next five figures.)

FIG. 2. Seeds of *Euterpe langloisii*.

PLATE II

FIG. 3. Seeds of *Livistona chinensis*.

FIG. 4. Seeds of *Trattinickia rhoifolia*.

PLATE III

FIG. 5. Seeds of *Ocotea wachenheimii*.

FIG. 6. Seeds of *Aniba firmula*.

PLATE IV

FIG. 7. Oilbird nests in the Arima gorge, showing eggs and small young, and seeds of *Ocotea caracasana* (smooth, shiny and spindle-shaped) and *Jessenia oligocarpa* (larger, streaked) round the edges of the nests.

FIG. 1
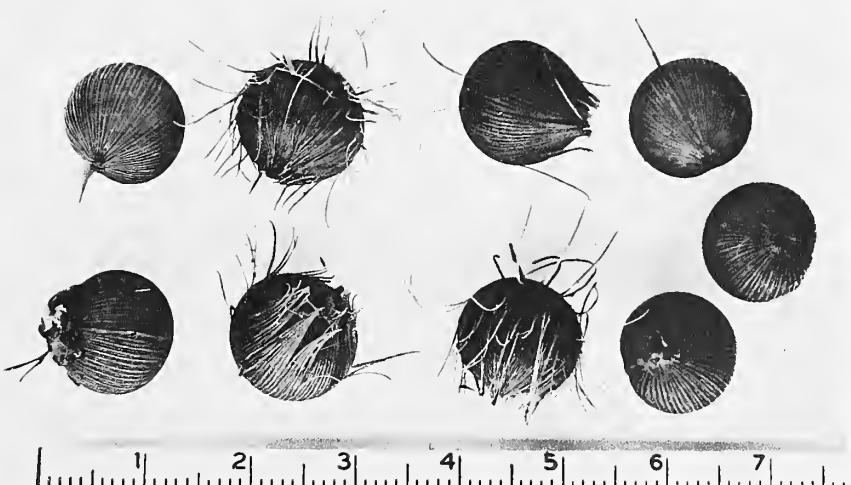
FIG. 2

THE NATURAL HISTORY OF THE OILBIRD,
STEATORNIS CARIPENSIS, IN TRINIDAD, W.I.
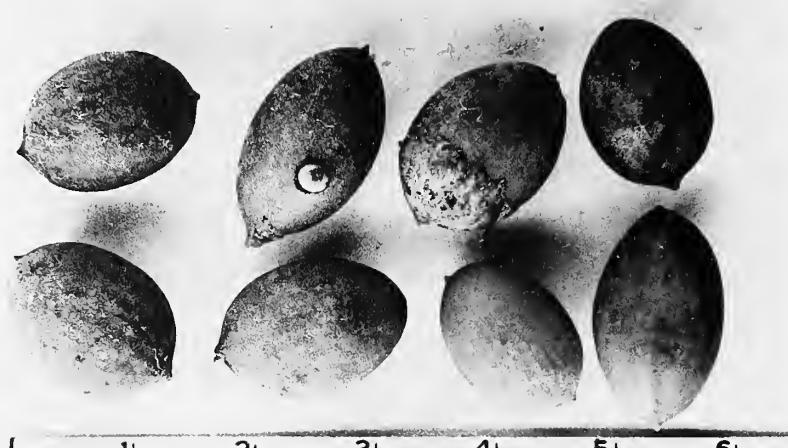
FIG. 3

FIG. 4

THE NATURAL HISTORY OF THE OILBIRD,
STEATORNIS CARIPENSIS, IN TRINIDAD, W.I.

FIG. 5

FIG. 6

THE NATURAL HISTORY OF THE OILBIRD,
STEATORNIS CARIPENSIS, IN TRINIDAD, W.I.

FIG. 7

THE NATURAL HISTORY OF THE OILBIRD,
STEATORNIS CARIPENSIS, IN TRINIDAD, W.I.

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